EFFECT OF NUTRIENT AVAILABILITY AND COMPETITION CONTROL ON GROWTH AND C, N, AND P DYNAMICS IN LOBLOLLY PINE AND SLASH PINE PLANTATIONS IN NORTH-CENTRAL FLORIDA

A Dissertation

by

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ABSTRACT

The pine plantations of the southern United States play a major role in the economies and carbon cycling of the region. Ensuring their long-term productivity will rely on information regarding the ecosystem nutrient response to management approaches. Many studies have assessed the effect of silvicultural practices on growth and ecosystem nutrient budget in the current rotation, but little is known about the carry-over effects of treatments used in a rotation on a subsequent rotation's growth and nutrient dynamics. The purpose of this study was to elucidate how growth and ecosystem carbon, nitrogen, and phosphorus pools respond to species selection loblolly pine and slash pine, fertilization (F), competition control (W) and F+W treatments in one rotation and their carry-over to the subsequent rotation. Two experimental sites, IMPAC and G8, located in north-central Florida were evaluated. I evaluated total tree biomass, soil total carbon, nitrogen and phosphorus, extractable NH_4^+, NO_3^- and PO_4^{3-}. Allometric equations were used to estimate total biomass and combustion, inductively coupled plasma atomic emission spectroscopy, KCl and Mehlich III extraction methods were used to quantify carbon and nitrogen, phosphorus, extractable nitrogen and phosphorus, respectively.

At the end of a 25-year rotation at the G8 site, total tree biomass increased in the order: Control < F < W < FW, with only the FW treatment significantly exceeding the Control. N and P pools and soil NH_4^+, NO_3^- and PO_4^{3-} were increased by F. Early growth up to age 3 years of the second rotation exceeded the first rotation by ~2-fold. Retreated F and W increased biomass tree growth, while the CF treatments increased growth and CW decreased growth.

At the IMPAC site, forest floor phosphorus pools were larger in loblolly pine compared to slash pine. The fertilization of these forests appears to have the potential to increase phosphorus

pools and availability across rotations, while competition control alters nitrogen dynamics, potentially through an increase in altered organic matter chemistry and nitrogen immobilization potential. Silviculture can increase or decrease growth across rotations, but the effects early in rotation are much smaller than the progress made in genetics and silviculture.

DEDICATION

To my brother **Aimable Ngenzi** and other brave young men and women, thank you for putting your life on the line to save many lives. We forever indebted to you and you will remain in our hearts until we meet again!

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This research was supervised by a dissertation committee consisting of Dr. Jason Vogel (advisor) and Dr. Thomas W. Boutton (co-advisor) of the Department of Ecosystem Science and Management, Dr. Frank M. Hons and Dr. Jacqueline A. Aitenkhead-Peterson of the Department of Soil and Crop Sciences at Texas A&M University, College Station, TX and Dr. Eric J. Jokela of University of Florida, Gainesville, FL.

All work of this dissertation was completed by Ignacie Tumushime, under the advisement of Dr. Jason Vogel and Dr. Thomas Boutton of the Department of Ecosystem Science and Management at Texas A&M University, College Station, TX.

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CHAPTER I

INTRODUCTION

Forestlands cover about 771 million ha in North America and currently store 170±40 Pg C, of which more than 70% is soil organic matter and litter (Birdsey et al. 2007). Forest ecosystems in the United States have been estimated to be a net sink of C of 0.27 Pg C/year (Birdsey et al. 2007), offsetting about 13% of fossil fuel emissions from the Northern hemisphere (Goward et al. 2008). This carbon sink function is an important ecosystem service provided by forests as it plays a major role in limiting CO_2 increases in the atmosphere through photosynthesis (Bonan 2008, Canadell and Raupach 2008), as CO_2 and other greenhouse gas emissions are widely believed to be the main drivers of climate change and global warming (IPCC, 2007). Moreover, forests are estimated to store up to 80% of C of all aboveground biomass worldwide (Dixon et al. 1994). A critical question is how human management decisions will affect this stored C and the C cycle of forests.

Most Northern hemisphere forestlands are located in the United States of America and Canada and more than 50% of total forests area is used to produce timber for forest products (Food and Organization 2006). Of these forests, the managed pine forests of the southeastern United States are the most intensely managed forests on the continent (Schultz 1997, Fox et al. 2007a), with management strategies that have served as a model for the rest of the world. These forests are found on ~60% of the total land area (Wear and Greis 2002c). Of these forests, managed plantations of loblolly *(Pinus taeda* L.) and slash pine (*Pinus ellioti var.elliotti* Engelm) are ~30% of the land area (Fox et al. 2007a, Fox et al. 2007b), with loblolly pine being the dominant commercial species (Johnsen et al. 2001, Adegbidi et al. 2002). Besides this economic provision, these plantations are valuable for the other ecosystems services that they provide such as non-timber products (e.g. pine straw for landscaping mulch), clean water and air, wildlife and fish habitat, recreation, aesthetics and preservation of biodiversity (Fox 2000). Despites the urban land expansion that reduces the forestland, improved productivity of intensively managed pine plantations has increased timber production in the region (Wear and Greis 2002a). The production of timber from these forests is estimated to be 18% of the global industrial timber supply (Prestemon and Abt 2002), with a prediction of a production increase of 67% in the coming decades (Prestemon and Abt 2002, Wear and Greis 2002a). The managed pine forests are important components of the regional economy where the forest products industry is responsible of about 6% of jobs and 8% of income, and the recreation-based tourism creates 0.6 - 2.9 % of jobs (Wear and Greis 2002a). In addition, these forests are reported to sequester nearly 13% of greenhouse gas emissions (Han et al. 2007), suggesting the benefits of the United States to meet the global policy commitments related to C sequestration (Johnsen et al. 2001). Previous research suggests a great potential C sequestration by fast-growing managed pine plantations of that region (Johnsen et al. 2001).

As the global human population continues to increase rapidly, demand for forest products and services is increasing simultaneously while natural forest lands are decreasing as they are lost for agriculture purposes and urbanization (Wear and Greis 2002a). Global demand for wood products has been increasing at 1.5 to 2% annually (FAO,1999), while environmental regulations have restricted harvest of natural stands and the supply of timber and other forest products has declined for several decades (Food and Organization 2006). By producing more wood on less area, intensive forest management practices will be an important strategy to raise the possibility that pressures for harvesting within natural forest can dramatically be reduced. Moreover, the managed forest serve to meeting the high demand for forest products and improving the ability of forests to capture carbon (Sedjo 2001, Bowyer 2007). Intensively managed forests have the potential to continuously produce a renewable stream of industrial raw materials that are more environmental friendly than other raw materials (Bowyer 2007).

The southeastern US managed pines receive multiple silvicultural treatments, including site preparation, planting of genetically improved pine seedlings, fertilization, and competition control (Farnum et al. 1983, Snowdon and Waring 1984, Allen et al. 1990, Colbert et al. 1990, Jokela 2004, Wagner et al. 2006, Jokela et al. 2010), which have dramatically increased the growth rates and biomass accumulation of intensively managed pine species (Jokela 2004, Jokela et al. 2010). Fox et al. (2007a) documented that the intensive management practices have tripled the forest production in the last 50 years, which increased financial returns to the landowners (Yin et al. 1998, Yin and Sedjo 2001, Allen et al. 2005).

Increasing forest productivity and carbon capture effectively can be done using a number of silvicultural practices. Factors that limit tree growth are ameliorated by the use of intensive silvicultural practices like site preparation, understory control, fertilization, planting of genetically improved seedlings and manipulation of stand density (Fox 2000, Jokela 2004). The combined use of all silvicultural practices can improve yields by more than double compared to extensively managed forests (Allen et al. 1990, Colbert et al. 1990, Neary et al. 1990). A common silvicultural practice is to alleviate nutrient deficiencies, imbalances and limitations through fertilization (Duzan et al. 1982, Gent et al. 1986, Allen 1987, Jokela et al. 1991, Jokela 2004, Albaugh et al. 2009) or competition control (Subedi et al. 2014).

Nitrogen and Phosphorus are generally accepted to be limiting nutrients to ecosystem productivity (Vitousek et al. 2010), and in southeastern United States forests, both N and P are widely applied as fertilizer (Fox et al. 2007a). The sources of P fertilizer include diammonium phosphate (DAP), triple superphosphate (TSP) and rock phosphate, with DAP being the most widely used source of P fertilization at time of planting (Fox et al. 2007a). Because both N and P become deficient nearly at the canopy closure in plantations growing on most soils of the south-eastern US (Fox et al. 2007a), fertilization at mid-rotation, in addition to at the time of planting, has become a common silvicultural practice. Numerous studies have reported that fertilization with N and P near establishment (Jokela et al. 2000; Carlson et al. 2014) or at mid rotation (Rojas 2005) increased loblolly pine productivity. Other growth limiting nutrients, besides N and P, have been inferred from general agronomic models of plant nutrition (Marschner et al. 1986). For pines, micro-nutrient deficiency such as copper (South et al. 2004), manganese (Jokela et al. 1991) and calcium (Huntington et al. 2000) has been documented in the southeastern United States (Carlson et al. 2014). For instance, Ca deficiencies were alleviated by liming in different sites such as the North Carolina Piedmont (Van Lear 1980), coastal plains of South Carolina (MacCarthy and Davey 1976) and Virginia (Fox et al. 2005). Additionally, a decrease in growth could be related to the antagonism between nutrients, where natural soil supply of one element interfered with N or P uptake (Van Lear and Smith 1972). Understory plants often accumulate relatively large stores of macro- and micronutrients (Subedi et al. 2014), suggesting the competing understory might induce deficiencies in planted pine trees.

Competition control is also a common component of silviculture in the southeastern United States as it increases productivity either when applied alone or when combined with fertilization (Jokela et al. 2000, Jokela et al. 2010). Competition control alleviates shading effects on forest growth, competition for different nutrients (Nambiar and Sands 1993, Collet et al. 1996, Zhang et al. 2012) , and can reduce the release of allelochemicals in the rhizosphere that may inhibit planted pine (Putnam 1988). It also alleviates the competition for available natural resources (soil nutrients and water). Studies have also revealed that combining fertilization with competition control can dramatically increase pine growth rates and biomass accumulation in pine forests (Jokela 2004, Jokela et al. 2010). With competition control, the composition of litter fall and the forest floor are dominated by pine needles and this change has corresponded to decreases in inorganic N (Rifai et al. 2010) and P (Polglase et al. 1992b). Thus, there is a possibility that competition control and fertilization could interact to affect site productivity.

Of the types of silvicultural treatments applied to forests, P fertilization has repeatedly shown potential to increase site productivity across rotations (Pritchett and Comerford 1982). In a study conducted on P deficient soils of both Georgia and New Zealand, Comerford et al. (2002) documented a significant effect of P fertilization that lasted into both the forest floor and mineral soil 29 and 22 years after fertilization at the above sites, respectively. Moreover, Gentle (1986) reported that elevated levels of available P and a continued growth response in subsequent rotations, demonstrating a long-term increase in soil quality. The high residency time of P in soil could also result in N demand in microbes (Craine et al. 2007) and plants (Treseder and Vitousek 2001), increasing N stabilization in the ecosystem, particularly, in forest floor and soil organic matter. Additions of inorganic nutrients in amounts that are relatively large in comparison to the pool of available soil nutrients can have a long-term impact on site productivity (Fox 2000), and sustained increases in rates of nutrient cycling and mineralization following fertilization have also been documented (Maimone et al. 1991, Dalla-Tea and Jokela 1994) which contribute to the long-term increase in soil quality.

Nutrients that are lost from an ecosystem are an economic liability and can worsen other environmental issues (Nolan et al. 1997, Vitousek et al. 1997, Carpenter et al. 1998). For instance, N that is not up-taken by plants and microbes or fixed by soil exchange sites is susceptible to leaving the ecosystem, increasing N_2O in the atmosphere. In addition, NO_3^--N may leach and contribute to groundwater and streams pollution with negative effects on human and animal health. Excess P may leach into deeper soils, become fixed into chemical forms that are inaccessible to plants and microbes, and/or be lost to streamflow via runoff, thereby causing eutrophication in fresh water bodies. Based on a mass balance approach, Will et al. (2006) estimated that ~90% of applied N was retained while in excess of 100% of the added P was retained in a loblolly pine forest. In contrast, more than half of applied N was lost from soil when fertilizer and competition control were applied together in a loblolly pine forest of north central Florida (Vogel et al. 2011). This suggests that fertilizer loss might be sensitive to when the understory vegetation is controlled, with the increased surface soil temperature increasing the NH_4^+ volatilization as NH_3, in particular when N is applied as urea. In order to minimize the cost of fertilizers, reduce nutrient loss, and protect the environment directly and through sustained productivity, the interactive effect of applied fertilizers and competition control on soil nutrient dynamics and their residual effect on the next rotation's productivity need to be better understood.

There has been a rapid increase in the productivity of southern US managed pine plantations over the last several decades because of improved genetics and silviculture (Fox et al. 2007b), and increases in CO_2 (McCarthy et al. 2010). Residual fertilizer could potentially meet some of the nutrient demands of these fast growing forests (Subedi et al. 2014), in particular during early rotation when nutrient demand is greatest for fine root and foliage development (Miller et al. 1995). In addition, the fast-growing pines have the potential to take up nutrients during the early years of the rotation before they leave the ecosystem. Alternatively, competition control without fertilizer additions could result in slower growth in the next rotation (Subedi et al. 2014); an effect that could be a transient response to changes in forest floor chemistry (Polglase et al. 1992a, Vogel et al.

2011). Optimizing silviculture applications to the current growth potential of southern pine forests requires an understanding of these and other carry-over effects.

An additional change in silviculture has occurred with a shift in species selection across the range of southern pines. Since the early 21st century, there has been a trend for more loblolly pine being planted than slash pine in the southeastern United States (South and Harper 2016), and, overall, pine plantations are expected to continue to increase in extent by the year 2040 across the region (Wear and Greis 2002a). These trends suggest that many plantations that were once slash pine, and as well as new plantations, will in the future be loblolly pine plantations. This transformation of the region's plantations toward dominance by one species could affect ecosystem C and nutrient cycling, because of how these species interact with silvicultural treatments. For example, in a comparison of the two species' C accumulation, a slash pine stand receiving only competition control stored more C in tree biomass at the end of rotation than did loblolly pine stands receiving competition control, fertilization, and fertilization plus competition control (Vogel et al. 2011). Some studies have reported that an increase in fertilization intensity negatively affects slash pine biomass relative to loblolly pine at the same site, often because of greater pitch canker (*Fusarium circinatum* Nirenberg & O'Donnell) infection in slash pine (Roth et al. 2007, Zhai et al. 2015). The mineralization of P from litter has also responded differently to silvicultural treatments for the two species (Polglase et al. 1992c), and relative amounts of fertilizer N retention have differed in response to whether competition control and fertilization were separate or combined for the two species (Vogel et al. 2011).

There has been increasing scientific and forest industry interest in the carry-over effects and sustainability of silvicultural practices across multiple rotations (Subedi et al. 2014). Studies have generally focused on the effect of fertilizer or competition control on a single species' growth in the next rotation (Comerford et al. 2002), often in the context of the effect of fertilization on nutrient pools (Gentle et al. 1986, Everett and Palm-Leis 2009, Kiser and Fox 2012). Loblolly pine litter generally has higher nutrient (N and P) concentrations than slash pine (Polglase et al. 1992b, Dicus and Dean 2008), possibly leading to higher N and P mineralization in stands of loblolly pine than in slash pine. Previous work documented that greater stand volume in loblolly pine than slash pine plantations was positively correlated with N mineralization (Dicus and Dean 2008). In addition, Polglase et al. (1992) found greater P release from the decomposing litter of loblolly pine than slash pine, possibly explaining its greater productivity, and highlighting the potential species effect on long-term site productivity.

The objectives of this research were to: 1) compare and contrast the interacting effects of species selection (slash pine vs. loblolly pine), fertilization and weed control treatments on ecosystem C and nutrient dynamics at the end of rotation and 2) quantify whether these silvicultural treatments have a carry-over effect on the next rotation's productivity. The results of this study will contribute to the information that forest industry stakeholders can use to adjust management prescriptions that would ultimately save them money, increase forest growth, and reduce nutrient losses from forest management practices.

CHAPTER II

EFFECTS OF FERTILIZATION AND WEED CONTROL ON TREE GROWTH AND C, N AND P DYNAMICS IN A LOBLOLLY PINE PLANTATION IN NORTH CENTRAL FLORIDA

II.1. Synopsis

The growth of pine plantations in the southeastern US is often limited by nutrient availability and vegetation competition. Fertilization and the control of understory competition are commonly used to overcome these limitations, but it is unclear how these practices affect C cycling and the sustainability of pine plantations. Carbon, N and P accumulation and extractable nutrients for a loblolly pine *(Pinus taeda* L.) plantation at age 25 years were assessed for treatments with different N and P fertilizers (diammonium phosphate (F_{DAP}) and triple superphosphate (F_{TSP})), competition or weed control (W) and the combined application of treatments ($F_{DAP}W$ or $F_{TSP}W$). Tree biomass was estimated from multiple forest inventories collected throughout the rotation, and samples from pine tissues, forest floor (Oi, Oe+Oa), and soils (0 - 10, 10 - 20, 20 - 50 and 50 - 100 cm) analyzed for C, N and P concentrations. Tree biomass C ranged from 163 to 205 Mg C ha^{-1} at the end of rotation, and approached significant increases for treatments relative to the control, where the F and W treatments were combined for $F_{DAP}W$ ($p=0.131$) and $F_{TSP}W$ ($p = 0.069$). Other C pools (forest floor and soils) were not significantly different from the control for any treatment. Combining the F and W treatments significantly ($p<0.05$) increased nutrient uptake for stem N content, and bark and foliage P content.

Fertilization as a main effect did not significantly increase nutrient contents in pine tissues, but did increase N and P content in the Oe+Oa horizons and some soil depth intervals. The W treatment alone most often decreased soil extractable N (NH_4^+, NO_3^-) relative to the control, while fertilization either alone or in interaction with W increased both extractable N and P. Fertilization increased nutrient availability, but for this inherently productive site, competition control was required for these nutrients to increase pine biomass accumulation.

II.2. Introduction

In the southeastern United States, forests are found on ~60% of the total land area (Wear and Greis 2002b). Of these forests, managed plantations of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliotii* Engelm.) are ~30% of the land area (Fox et al. 2007b), with loblolly pine being the dominant commercial species (Johnsen et al. 2001, Adegbidi et al. 2002). The southeastern US managed pines are among the most intensively managed forests on the continent (Schultz 1997, Fox et al. 2007b), with managers using strategies that have served as a model for other parts of the world.

The forests in the region also play a crucial role in regional carbon dynamics as they sequester nearly 42% of anthropogenic greenhouse gas emissions (Han et al. 2007, Lu et al. 2015). Previous research suggests a great potential for C sequestration by fast- growing managed pine plantations (Johnsen et al. 2001), with some variation in C sequestration based on the approaches used to increase pine plantation growth (Shan et al. 2001, Vogel et al. 2011). For example, increased growth rates can result from planting trees at fixed spacing, using mechanical and chemical site preparation, deploying genetically improved seedlings, along with fertilizer additions and the control of competing understory vegetation (Fox et al. 2007b). Of these approaches, fertilizer additions have increased both above- and belowground pools of C (Shan et al. 2001, Vogel et al. 2011), but at experimental rates that are above those used in normal forestry operations.

Forest growth potential in the southeastern US is often limited by soil nutrient availability, which limits leaf area production (Fox et al. 2007b). Fertilization increases plant nutrient uptake of N and P, accelerating tree growth and stand development (Fisher and Garbett 1980, Albaugh et al. 2004, Martin and Jokela 2004). The relative effect of fertilization is generally greatest where the background levels of soil N and P are in low supply (Zhao et al. 2014), which is the case for many soil types in the southeastern US (Phelan and Allen 2008). As a result, N and P are widely applied as fertilizers to commercial pine plantations in this region (Albaugh et al. 2007, Fox et al. 2007b).

Control of competing vegetation, primarily using herbicides, has accelerated tree growth and stand development to levels near that of fertilization alone (Jokela et al. 2010). The control of competing vegetation generally occurs in southern pine plantations at planting or early stand establishment (age 1-3 years), and may occur again at some point later in the rotation (age ~8-15 years). Early in stand development competition control may relieve shading effects on pine seedling growth, while for both early- and mid-rotation herbicide applications, the treatment may reduce the competition for available soil nutrients and water (Collet et al. 1996, Zhang et al. 2012).

With the potential effect of forest plantations on regional C dynamics, it is important to understand how ecosystem C pools are affected by the silvicultural treatments used to increase pine growth. With competition control, available nutrients might support more woody tissues in pine biomass than in understory plants (Will et al. 2006, Vogel et al. 2011, Subedi et al. 2014), resulting in greater aboveground biomass C accumulation. Moreover, increased net primary productivity from fertilization increases detrital C inputs to the forest floor and soil, while competition control shifts nutrient resources from the understory to the overstory. There is mixed evidence that the forest floor loses C with competition control (Vogel et al. 2011), which could be related to the greater insolation to the forest floor and the resulting warmer temperatures, and faster decomposition rates. Soil C often increases following fertilizer applications (Johnson 1992, Schlesinger 2000), which could be from increased inputs of root material, litter fall, or inhibited microbial decomposition. Combining fertilization and competition control has had complex effects on C accumulation in pools other than tree biomass. With the combined application of fertilization and competition control, a decrease in the C stored in the forest floor (Vogel et al. 2011) and soils (Shan et al. 2001) has been observed.

Carbon and nutrient dynamics can interact with the types of fertilization or competition control treatments used. For example, fertilization with one nutrient can affect the dynamics of other nutrients in the ecosystems (Shaver and Chapin III 1980, Miller 1981, Shaver et al. 1992), as with N and P affecting the availability and accumulation of the other nutrients (Harding and Jokela 1994). Additions of N allow organisms to produce more extracellular phosphatase enzymes that cleave ester-P bonds in soil organic matter, increasing availability of P (Vitousek et al. 2010). Conversely, additions of P mixed with micronutrients required for nitrogenase enzyme (e.g. Fe and Mo) and nodules formation on N_2 fixing species (e.g. B) (Vitousek and Howarth 1991) have the potential for increasing symbiotic and asymbiotic N fixation (Wurzburger et al. 2012) that contribute to N accumulation in ecosystems. Fertilization with N and P, and P alone has significantly increased biomass C and P, and also K and Ca accumulation in surface soil (Harding and Jokela 1994).

Contrary to fertilization, competition control has been shown to have a negative effect on nutrient accumulation in pine plantations. Previous studies have found that understory competition control decreased pools of soil N (Sartori et al. 2007, Rifai et al. 2010, Vogel et al. 2011) and also inorganic N (Rifai et al. 2010) and P (Polglase et al. 1992b). The effect of competition control on nutrient dynamics may depend on understory nutrient demands, tissue chemistry, or whether tree growth is able to acquire the nutrients made available by the absence of an understory.

The overall objective of this study was to assess the effects of fertilization, competition control and the combined application of these treatments on total biomass C, N and P accumulation in vegetation, forest floor, and soil at the end of a 25-year-old loblolly pine plantation rotation. I hypothesized that the increase in ecosystem C accumulation would occur with N and P fertilization and, in particular, that fertilization would increase the N and P accumulation in vegetation, forest floor, and soil, but that competition control alone would reduce C and nutrients in the forest floor and soil. The amount of C, N, and P found in forest floor and soil pools at the end of harvest would likely affect tree growth in the next rotation (Subedi et al. 2014), and affect the need for repeat applications of fertilizer across rotations.

II.3. Material and methods

II.3.1 Study overview and site description

The research area was originally one of 25 experimental sites established in 1987 by the University of Florida's Cooperative Research in Forest Fertilization program in cooperation with Auburn University's Silviculture Herbicide Cooperative. The study's goal was to evaluate the main effects and interactions of fertilizer and competition control treatments applied at establishment and at mid-rotation on the potential growth of managed pine forests (Johnson 1992, Jokela et al. 2000). The study site for this experiment was located near Palatka, FL (29°38′N, 81°39′W).

The nearby city of Palatka, FL receives a mean annual precipitation of 1279 mm and has a mean annual temperature of 21.2 °C (NOAA, 1984 - 2013). The climate of the site is sub-tropical (i.e. warm and humid). The soils were designated as poorly drained Pomona fine sands (sandy, siliceous, hyperthermic Ultic Alaquods). Soil properties are summarized in table 2-1. Soil pH of the site is 4 - 5. Surface particle size analysis (Bouyoucos 1962) for the soils at this site indicated 84% sand, 10% silt and 6% clay on average in the upper 1 m. The study area was sloped ~2% and fell within the flood zone of a river 280 m from installation center, and it was 5 m above sea level. Prior to study establishment, the site was an unmanaged pine flatwoods forest with predominately slash pine (*Pinus elliottii* Engelm.) in the overstory. The understory vegetation was composed of both woody and herbaceous species. The herbaceous species were dominated by chalky bluestem (*Andropogon capillipes* Nash.), panic grasses (*Panicum* spp. and *Dichanthelium* spp.), dogfennel (*Eupatorium capillifolium* (Lam.) Small), and sedge (*Cyperus* spp.) and the woody species included gallberry (*Ilex glabra* (L.) Gray), sawtooth palmetto (*Serenoa repens* (B.) Small.), blueberries (*Vaccinium* spp.), St. John's-wort (*Hypericum fasciculatum* Lam.), and runner oak (*Quercus pumila* Walt.).

Table 2-1. Mean (±SE) bulk density, soil particle distributions and pH averaged across all study plots at the time of sampling.

Soil depth (cm)	Treatment	Soil texture (g kg^{-1})			pH
		Sand	Silt	Clay	
0-10	C	839 (7)	112 (8)	49 (1)	4.6 (0.06)
	F_{DAP}	853 (14)	102 (6)	45 (10)	4.7 (0.11)
	W	842 (7)	113 (4)	46 (10)	4.6 (0.06)
	F_{DAP} W	827 (17)	126 (14)	48 (7)	4.5 (0.10)
	F_{TSP}	850 (9)	101 (6)	49 (4)	4.6 (0.06)
	F_{TSP} W	843 (15)	311 (20)	46 (8)	4.6 (0.14)
10-20	C	860 (12)	102 (10)	37 (2)	4.8 (0.12)
	F_{DAP}	854 (9)	104 (2)	42 (6)	4.9 (0.16)
	W	849 (13)	111 (7)	41 (7)	4.7 (0.12)
	F_{DAP} W	867 (8)	92 (4)	41 (4)	4.5 (0.08)
	F_{TSP}	850 (13)	101 (8)	49 (8)	4.7 (0.05)
	F_{TSP} W	857 (1)	102 (3)	41 (3)	4.7 (0.15)

Table 2-1. Continued

Soil depth (cm)	Treatment	Soil texture (g kg^{-1})			pH
		Sand	Silt	Clay	
20-50	C	884 (2)	79 (4)	37 (3)	5.5 (0.17)
	F_{DAP}	882 (10)	81 (8)	36 (4)	5.9 (0.17)
	W	875 (4)	93 (1)	32 (5)	5.5 (0.16)
	F_{DAP} W	881 (13)	77 (11)	42 (4)	5.1 (0.12)
	F_{TSP}	866 (11)	96 (8)	38 (3)	5.4 (0.10)
	F_{TSP} W	874 (14)	87 (11)	39 (3)	5.3 (0.22)
50-100	C	789 (21)	89 (3)	122 (23)	5.1 (0.08)
	F_{DAP}	801 (24)	90 (6)	109 (25)	5.2 (0.10)
	W	825 (10)	100 (9)	75 (19)	5.2 (0.10)
	F_{DAP} W	836 (15)	93 (8)	71 (13)	4.9 (0.08)
	F_{TSP}	818 (39)	83 (2)	99 (40)	5.0 (0.04)
	F_{TSP} W	822 (25)	85 (5)	92 (23)	4.9 (0.11)

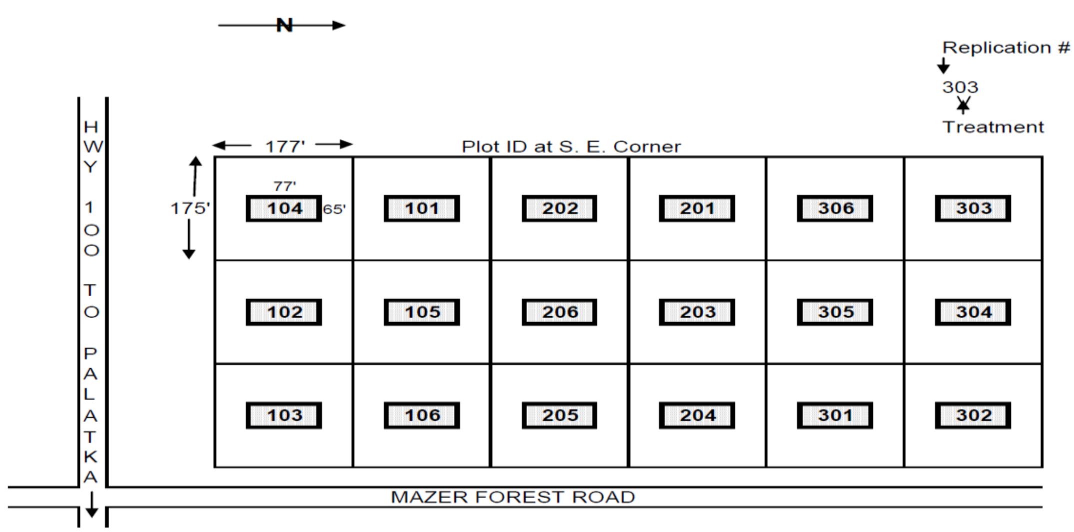

Figure 2-1. G-8 experiment and treatments.

II.3.2 Study Design and Treatments

The experiment was established as a randomized complete block design (Figure 2-1) with six treatments and three blocks: Control (C), fertilization with diammonium phosphate (F_{DAP}), competition or 'weed' control (W), fertilization with diammonium phosphate plus competition control ($F_{DAP}W$), fertilization with triple superphosphate (F_{TSP}), and fertilization with triple super-phosphate plus competition control ($F_{TSP}W$) (Table 2-2). The site was mechanically prepared using a single pass bedding treatment and it was located on a recently harvested pine plantation that had not received any fertilizer additions (Jokela et al. 2000). For the competition controls plots, early weed control occurred at establishment using Oust XP and Velpar L. at application rates of 0.046 kg ha^{-1} and 0.384 kg ha^{-1}, respectively. At mid-rotation (age 9-10 years), Garlon (1.16 kg ha^{-1}) and Arsenal (0.184 kg ha^{-1}) were applied to the W and FW plots (Table 2-2). The planted loblolly pine seedlings were first-generation, open pollinated material that was selected for better growth and fusiform rust (*Cronartium fusiforme* Hedg.) resistance.

Table 2-2**.** Fertilizer application rates (kg ha^{-1}) and types of competition control and timing used for the loblolly pine experimental site.

Treatment	At establishment	Age 9-10 years
C	No fertilization or competition control	No fertilizer or competition control
F_{DAP}	50 N + 56 P	224 N + 44 P
W	Competition control only (Oust and Velpar)	Woody competition control only (Garlon and Arsenal)
$F_{DAP}W$	50 N + 56 P + competition control	Woody competition control + 224 N + 44 P
F_{TSP}	56 P + 15 Ca	224 N + 44 P at mid-rotation
$F_{TSP}W$	56 P + 15 Ca + competition control	Woody competition control + 224 N + 44 P

II.3.3 Tree Measurements and Biomass

Growth differences among treatments were assessed with biomass estimates derived from tree height (H), diameter at breast height (DBH, 1.37 m) as measured on all plots and trees. These measurements were conducted in multiple years over the rotation and then again in December 2012 prior to harvest. The data from the above mentioned inventories of DBH and height were used to predict the total aboveground biomass and its components using allometric equations developed for loblolly pine trees (Gonzalez-Benecke et al. 2014) where:

$$Biomass_{T,F,B,S} = C1 * DBH^{C2} * H^{C3}$$

The subscripts T, F, B, and S are equivalent to total biomass, foliage, branch and stem, respectively. The C1, C2, and C3 are the fit parameter estimates for each of the models for each component. An alternative equation form was used for bark biomass, where:

$$Bark = e^{(d1 + d2) * ln * (DBH * H)}$$

and d1 and d2 are the fit parameters (Gonzalez-Benecke et al. 2014). Site index (SI) at age 25 was estimated for each treatment from the average height of the upper quartile height of all trees. Quadratic mean diameter (Dq) trees per hectare was estimated as well.

II.3.4 Tissue Sampling and analysis

During the 25th year of the study, four randomly selected dominant and co-dominant trees from each plot were marked for tissue sample collection. Following harvest, foliage and branch tissues from those trees were collected from a branch located in the upper, middle, and lower crown positions. Stem disks were collected from the base of the tree and from the base of the live crown. Bark tissues were removed from the lower stem disc and stem wood was cut from outermost ring to the center pith from the upper stem and lower stem. The samples from the upper stem, lower stem, bark, branch and foliage were composited, oven-dried at 65°C, and ground in a Wiley Mill. The ground tissue samples were subjected to macro- and micronutrient analysis.

Forest floor material was collected for C and nutrients analyses. Six forest floor samples were randomly collected in each plot using a 20.3 cm diameter ring, organic horizons were re-moved, and then separated into Oi and Oe+Oa horizons. Each forest floor horizon was thoroughly mixed and a composite sample was created for each plot. For the Oe+Oa horizon, the sample was sieved on a 2 mm screen to separate forest floor, organic matter, and mineral soil. The mineral soil passed through the sieve and forest floor and organic matter collected on the top of the sieve were separated. Each component was oven-dried at 65°C and weighed. The forest floor samples (Oi and Oe + Oa) were then ground with a Wiley Mill to pass through a 1-mm sieve. The residual mineral soil was ground on a roller ball mill, analyzed for nutrients separately from the Oe+Oa layer and the estimated C, N, and P contents added back to Oe+Oa layer.

Three soil samples were collected by depth in each treatment plot using a 7.62 cm diameter auger (0 - 10 cm, 10 - 20 cm, 20 - 50 cm, and 50 - 100 cm). The samples were thoroughly mixed by plot, depth and location (bed and inter bed) to make a composite sample of about 1000 g that was used for nutrient analyses. These samples were weighed wet and stored in a walk-in cooler at

4 ˚C until analyzed. The soil was passed through a 2 mm sieve and roots and large woody fragments were removed from the top of the sieve and weighed. Soil pH was determined using a glass electrode on field-moist soil and a 1:2 soil to water ratio. Approximately 10% of the soil mass was oven-dried at 65 ˚C and ground on a roller ball mill for 48 hours until fully pulverized. To determine total soil P, 0.5 g of the ground and re-dried sample was dry-ashed in a muffle furnace at 450°C for four hours and mixed with aqua regia (1:3 $HNO_{3:}$ HCl) extracting solution (International Organization for Standardization (ISO 1997)). The extract was passed through Q5 filter papers pre-rinsed with 1% HNO_{3-} and analyzed using inductively coupled plasma atomic emission spectroscopy (ICP-AES).

The C and N concentrations in the soils and forest floor were analyzed by dry combustion using an elemental analyzer (Thermo Finnigan FLASH EA 1112). The standard soil N C reference material was used to assess the accuracy of the C and N measurements. This material consisted of purified and homogeneous lot of soil NC used in the calibration of elemental analyzers for determination of C and N concentrations. For mineral soils, carbonate removal via acidification was not performed because of the low pH 4 - 5 and highly weathered nature of the soils. For one block, bulk density values were estimated for the near surface soils (0 - 10 cm and 10-20 cm) with a corer, and the deeper horizons (20 - 50 cm and 50 - 100 cm) derived from pedo-transfer functions (A. Bacon unpublished data). The bulk density values used were 1.07 Mg m^{-3} (0 - 10 cm), 1.29 Mg m^{-3} (10 - 20 cm), 1.36 Mg m^{-3} (20 - 50 cm), and 1.44 Mg m^{-3} (50 - 100 cm). For the aboveground tissues, forest floor and roots, P was analyzed using an inductively coupled argon plasma unit (ICAP; Micro-Macro International Laboratory, Athens, GA). The 1,000 ppm phosphorus AA standard (Ammonium dihydrogen phosphate in water) was used to assess the accuracy of the P measurements. Tree biomass, forest floor, and soil N and P content were estimated by multiplying the dry mass by its corresponding N and P concentration. For C content, biomass was assumed to be 48% C for foliage and 50% C for branch, bark and stem wood tissues (Thomas and Martin 2012).

Relative differences in N and P availability were estimated with a one-time extraction performed on the soils collected at the end of the rotation. A 1 M KCl extractant was used for NO_3^- and NH_4^+ (Keeney and Nelson 1982) and a Mehlich III extractant (0.2 M CH_3COOH+0.25 M NH_4NO_3+0.015 M NH_4F+0.013 M HNO_3+0.001 M EDTA) was used to extract for available P (PO_4^{3-}) (Mehlich 1984). For the KCl extract, 3.0 g of soil was mixed with 30 ml of 1.0 M KCl extracting solution (soil: solution ratio 1:10) and shaken for 30 minutes (120 oscillation/minute). For the Mehlich III extract, about 3.0 g of soil was mixed with Mehlich III extracting solution (soil: solution ratio 1:10) and shaken for 5 minutes (120 oscillations/minute). Extracts were filtered through pre-rinsed Q2 filter papers into scintillation vials and frozen until chemical analyses were performed. Briefly, different chemical reactants were added to the samples that changed the colors of solutions. Salicylate and bleach solutions, Vanadium cocktail solution and Malachite Green solution were added to NH4$^+$, NO_3^- PO_4^{3-} samples, respectively. Solution color was blue green for NH_4^+, pale to bright pink for NO_3^- and green for PO_4^{3-} and were read at read at different wavelengths: 650 nm, 540 nm and 630 nm, respectively using the colorimetric method with a spectrophotometer EON Microplate reader (Biotek Instruments, Inc.). Prior to measurements, Ammonium standard, Nitrate standard and 1,000 ppm phosphorus AA standard were used to assess the accuracy for NH4$^+$, NO_3^- and green for PO_4^{3-}, respectively. For the incubation, soil moisture was brought to near field capacity and incubated on the benchtop at room temperatures (~22°C-25°C).

The soil texture of the site was analyzed using the Bouyoucos hydrometer method (Bouyoucos 1962). Briefly, 50 g of oven-dried at 65 °C soil that passed through a 2 mm sieve was mixed with a dispersing agent (2.5 N sodium hexametaphosphate, $(NaPO_30)_6$) and deionized water. A calibrated hydrometer was inserted into the suspended materials for 40 seconds to measure the amount of suspended silt and clay particles per liter while the sand particles are settled at the bottom of the cylinder. After 2 hours settling, another hydrometer reading was recorded to measure the amount of suspended clay particles per liter. The sand fraction was calculated based on the amount of clay and silt in a sample. The hydrometer readings were corrected according to the temperatures measured at both readings.

II.3.5 Statistical analyses

Data were analyzed as a randomized complete block experimental design (RCBD) using analysis of variance (ANOVA) and the SAS PROC MIXED model procedure (Littell et al. 1998) (SAS version 9.4, SAS Institute Inc., 1988). The fertilization treatments effectively shared a C and W treatment and, as a result, they are not directly compared in the analysis. Shapiro-Wilk test was conducted to assess the normality of data (Shapiro and Wilk 1965) and a square root transformation used for branch P data. The main effects and interaction of treatments, fertilization (F) and weed control (W), were estimated:

$$Yij = \mu i + F + W + F \times W + eij$$

where Y equals the biomass C, N, and P concentration and content in vegetation tissue, forest floor, and soil, and *eij* represents error associated with treatments and blocks. Blocks were treated as random effects. Where a significant interaction occurred between fertilization and weed control, a least squares difference comparison test was conducted with an alpha level of 0.05 used to designate significance. For simplicity, the end-of-rotation total tree biomass C was analyzed with a one-way ANOVA, where each treatment was contrasted with the control.

II.4. Results

II.4.1 Tree biomass

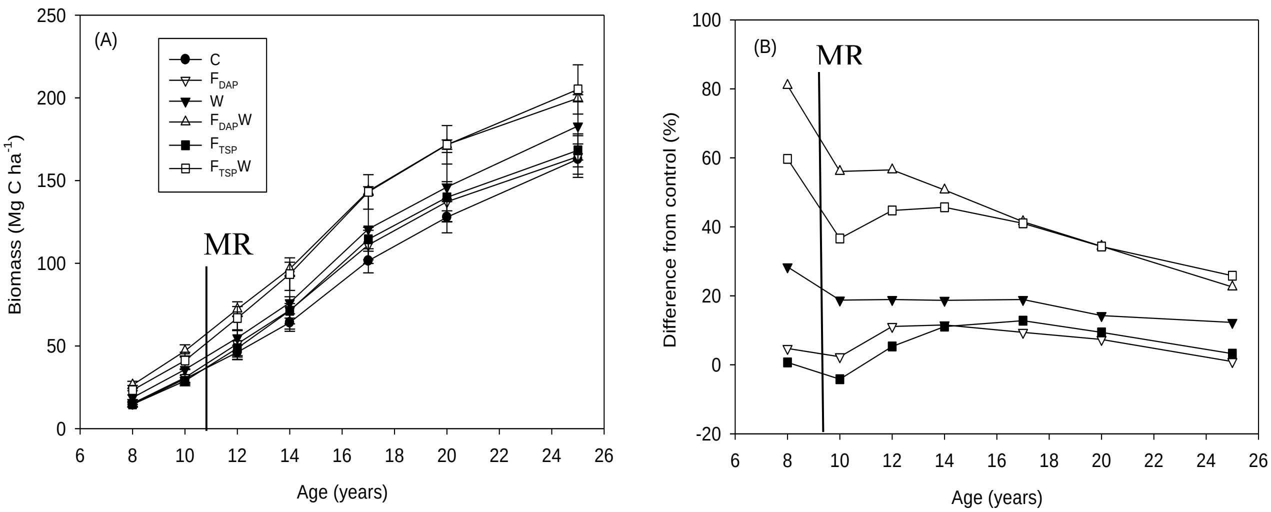

Figure 2-2. Total biomass accumulation (Mg C ha^{-1}) (A) and proportional difference from control (B) over time (mean ± SE) for a loblolly pine stand near Palatka, FL with a control (C), initial fertilization with diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP}), competition or 'weed' control only (W), and fertilization combined with competition control ($F_{DAP}W$ and $F_{TSP}W$). All fertilized treatments received a second application of their respective fertilization, or weed control, treatments at mid rotation (MR), between ages 9 -10 years.

Total biomass accumulation during the course of the rotation (Figure 2-1A) showed a consistent trend where the fertilization plus competition control exceeded other treatments, and the $F_{TSP}W$ and $F_{DAP}W$ treatments closely following one another (Figure 2-1A-B, Table 2-3). At the end of rotation, the $F_{TSP}W$ and $F_{DAP}W$ treatments accumulated 42 and 37 Mg C ha^{-1} more biomass C than the control plot. These treatments were marginally greater than the control ($F_{DAP}W$

(p=0.131) and $F_{TSP}W$ (p=0.069)) at the end of rotation (Table 2-2), but earlier in the study, the combined F+W treatments supported biomass C differences from control that exceeded 25% (Figure 2-1B). The mid-rotation application of fertilizer reversed or slowed downward trends in the F treated plots relative to the control 2 years (age 12) after application (Figure 2-2B). However, after age 16 the differences between treatments and the control started to decrease again and by the end of rotation the fertilizer only treatments were similar to the control for biomass (Figure 2-2). Indices of individual tree growth (Dq and SI) also tended to be greater in the fertilization plus competition control treatments in comparison to the control at the end of rotation but the differences were less pronounced than for biomass (Table 2-4). Although trees in the F_{DAP} treatment had the second greatest Dq after $F_{DAP}W$, the low tree density (Table 2-4) combined to produce a lack of a biomass response for this treatment.

Table 2-3. Statistical summary (p-values) comparing tree biomass C for fertilization (diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP})), competition control (W) and their combination ($F_{DAP}W$ or $F_{TSP}W$) treatments to the control (C) for a 25-year-old loblolly pine stand near Palatka, FL.

Contrast	DF	p-value
C vs. F_{DAP}	1	0.982
C vs. W	1	0.324
C vs. $F_{DAP}W$	1	0.131
C vs. F_{TSP}	1	0.813
C vs. $F_{TSP}W$	1	**0.069**

Effects with bold numbers are significantly different effects (Tukey’s HSD at alpha=0.10)

Table 2-4. Mean (±SE) tree density, quadratic mean diameter (Dq) and site index (SI) of a 25-year-old loblolly pine stand near Palatka, FL fertilized with diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP}), weed control (W), and fertilization combined with weed control (F_{DAP} W and F_{TSP} W) for a 25-year-old loblolly pine plantation.

Treatment	Density (trees/ha)	Dq (cm)	SI (m)
C	423 (29)	26.6 (1.2)	27.0 (0.6)
F_{DAP}	396 (20)	28.0 (1.2)*	27.6 (0.8)
W	423 (37)	27.6 (1.2)	27.2 (0.7)
F_{DAP}W	446 (24)*	28.2 (0.2)*	28.2 (0.3)*
F_{TSP}	457 (30)	26.5 (0.2)	27.2 (0.3)
F_{TSP}W	461 (27)*	27.7 (1.1)*	27.8 (0.5)*

* Significantly different relative to control (Tukey's HSD at alpha=0.05)

II.4.2 Carbon pools

The C content of aboveground biomass was greatest for stem wood (105.5-131.5 Mg C ha^{-1}) followed by branch (14.9 - 19.1 Mg C ha^{-1}), bark (12.3 - 15.0 Mg C ha^{-1}) and foliage (4.2 -5.3 Mg C ha^{-1}) pools (Table A-1). Although contrasts were not significant, fertilization plus competition control treatments tended to have greater C content than the fertilization or competition control alone for all components at the end of the 25-year rotation.

The forest floor C content ranged from 8.9 - 11.7 Mg C ha^{-1} and tended to be greater in the fertilized plots relative to the W only plots (Table A-1). However, no main or interaction effect for any treatment was significant for forest floor C accumulation.

Across all treatments, soil C content decreased from the 0 - 10 cm depth interval (28.2 - 33.5 Mg C ha^{-1}) to the 20 - 50 cm depth interval (9.6 - 22.4 Mg C ha^{-1}) and then increased in the 50 - 100 cm depth interval (48.8 - 69.0 Mg C ha^{-1}) (Table A-1). The response to treatments was not significant for any of the soil depth intervals. When C was summed across all depth intervals, $F_{DAP}W$ and $F_{TSP}W$ treatments showed increased C content by 13% and 30% relative to the respective fertilization alone treatments (F_{DAP} and F_{TSP}), and 8% and 17% greater than competition control, though those differences were not significant.

II.4.3 Nitrogen accumulation

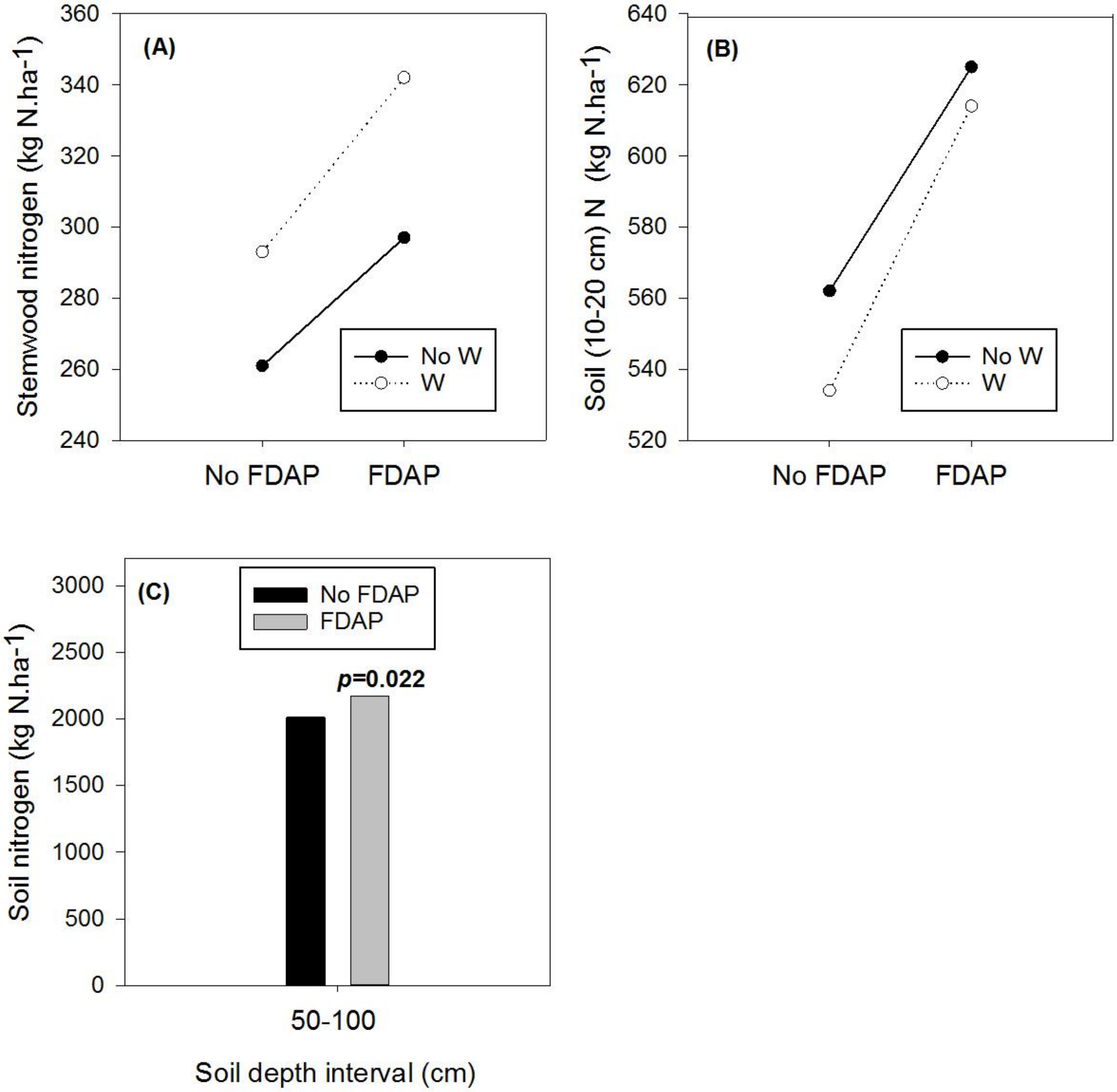

Figure 2-3. Significant F_{DAP} x W interaction effect for (A) stem and (B) soil (10-20 cm); F_{DAP} main effect for (C) soil (50-100 cm) for nitrogen accumulation (kg N ha^{-1}) in a 25-year-old loblolly pine stand near Palatka, FL.

Stem wood had the highest N content (262-376 Kg N ha^{-1}) followed by foliage (95 - 130 Kg N ha^{-1}), bark (31 - 44 Kg N ha^{-1}) and branches (23-33 Kg N ha^{-1}) (Table A-5). A positive interaction (p= 0.014) was found between F_{DAP} and W for stem wood N (Figure 2-3A), and for soil (10 - 20 cm depth interval) (p= 0.050) (Figure 2-3B), highlighting changes in scale. A significant F_{DAP} main effect (p= 0.022) was found for soil (50 - 100 cm depth interval) (Figure 2-3C), indicating a decrease of N content in the W plot treatments.

For the forest floor, fertilization alone with F_{DAP} (512 Kg N ha^{-1}) and F_{TSP} (556 Kg N ha^{-1}), had the highest N content compared with the W (378 Kg N ha^{-1}) and F_{DAP}W (485 Kg N ha^{-1}) and F_{TSP}W (540 Kg N ha^{-1}) treatments (Table A-4). Most of these trends were not significant, with only the F_{TSP} main effect reflecting an increase in forest floor N due to treatment (p= 0.021) (Figure 2-4A).

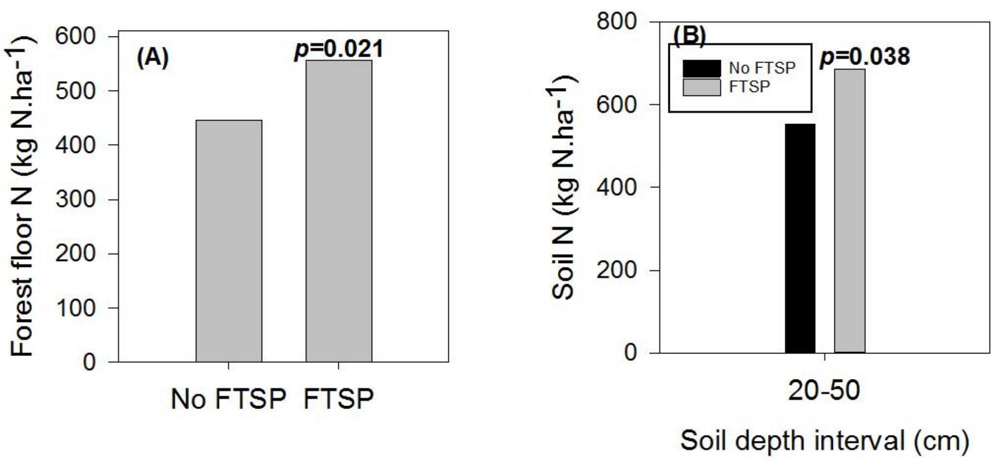

Figure 2-4. Significant F_{TSP} main effect for (A) forest floor and (B) soil (20 - 50 cm) for nitrogen accumulation (kg N ha^{-1}) in a 25-year-old loblolly pine stand near Palatka, FL.

In general, soil N pools followed the same trend as C, decreasing from the 0 - 10 cm depth interval (861 - 1204 Kg N ha^{-1}) to the 20 - 50 cm depth interval (533 - 887 Kg N ha^{-1}), then increasing in the 50 - 100 cm depth interval (1816 - 2453 Kg N ha^{-1}) (Table A-4). The latter result corresponded to the Bh horizons' location, which generally first occurred at the 20 - 50 cm interval, but was concentrated in the upper part of the 50 - 100 cm interval (personal observation). The F_{TSP}

main effect was significant in soil, reflecting increased N content relative to the unfertilized plots for the 20 - 50 cm (p= 0.038) depth interval (Figure 2-4B).

II.4.4 Phosphorus accumulation

Phosphorus accumulation in vegetation was highest for stem wood (9.9 - 18.3 Kg P ha^{-1}) followed closely by the foliage (8.0 - 12.9 Kg P ha^{-1}), branch (3.4 - 4.8 Kg P ha^{-1}) and bark (1.2 - 2.2 Kg P ha^{-1}) components (Table A-8). Because of the higher biomass of stems compared to the other vegetation components, stem P accumulation was the highest, although its P concentration was the lowest (Table A-4). The W main effect (p=0.043) increased P accumulation in the bark (Figure 2-5A).

For the forest floor P content, the sum of Oi and Oe+Oa was greater (29.5 - 47.8 kg P ha^{-1}) than the sum of all vegetation components (9.3 - 13.8 kg P ha^{-1}) (Table A-8). Some fertilization treatments (F_{DAP} and F_{TSP}) increased forest floor P pools, while competition control (W) decreased it. The F_{DAP} (p=0.002) treatment significantly increased the P content (Figure 2-5B). The effect of W (p=0.045) decreased P content for the Oi layer (Figure 2-4C). Also, the effect of W (p=0.034) decreased it for the Oe+Oa layer (Figure 2-5D). Similarly, the interaction effect of F_{DAP} and W (p=0.006) decreased P content for the Oi layer (Figure 2-4E). The significant F_{DAP} main effect (p=0.023) resulted in an increase of P accumulation in the soil (50-100 cm depth interval) (Figure 2-5F).

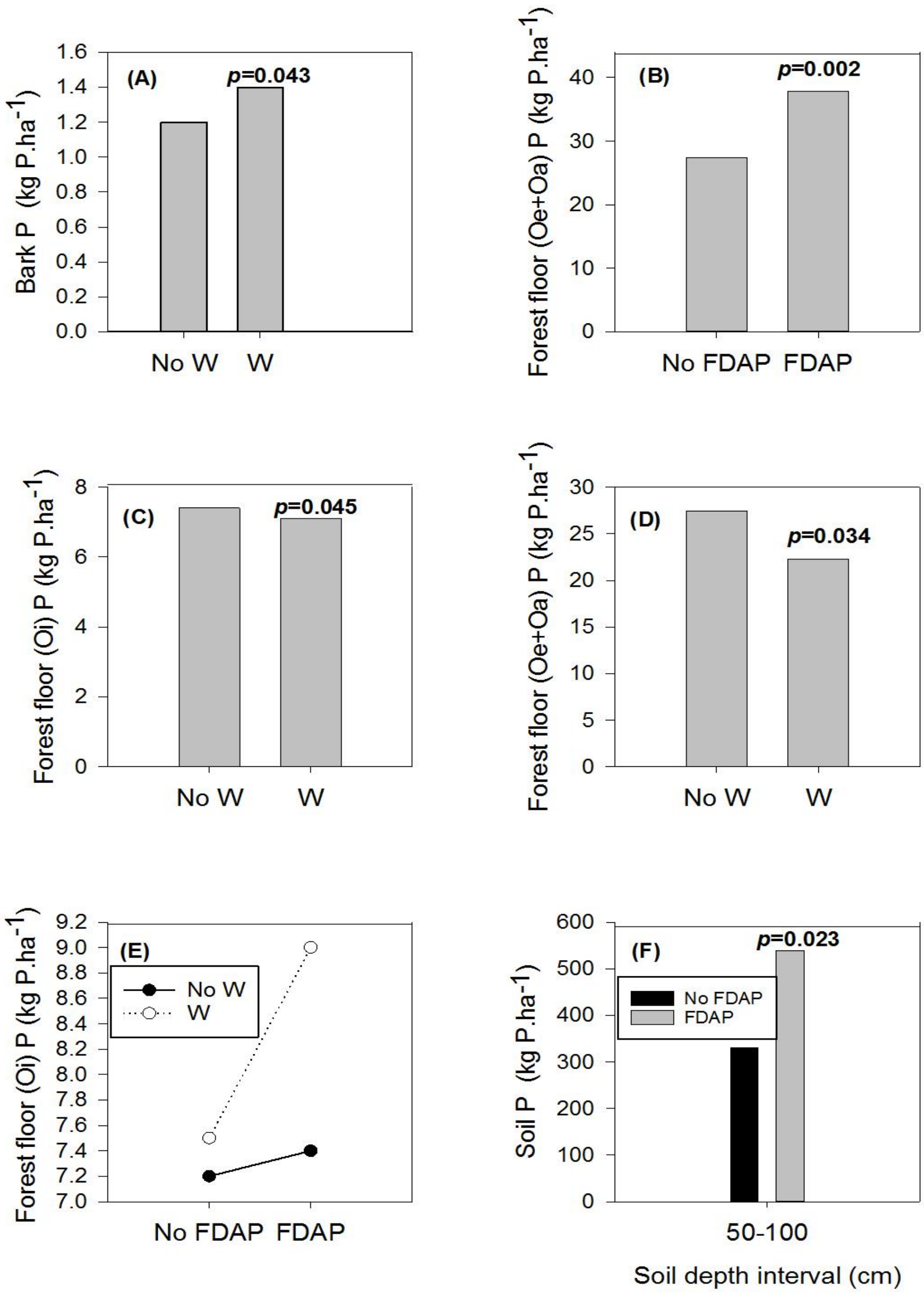

Figure 2-5. Significant W main effect for (A) bark; F_{DAP} main effect for (B) forest floor (Oe+Oa); W main effect for (C) forest floor (Oi) and (D) forest floor (Oe+Oa); F_{DAP} x W interaction for (E) forest floor (Oi) and F_{DAP} main effect for (F) soil (50 - 100 cm) for phosphorus (P) accumulation (kg P ha^{-1}) in a 25-year-old loblolly pine stand near Palatka, FL. Significant contrasts denoted in figures.

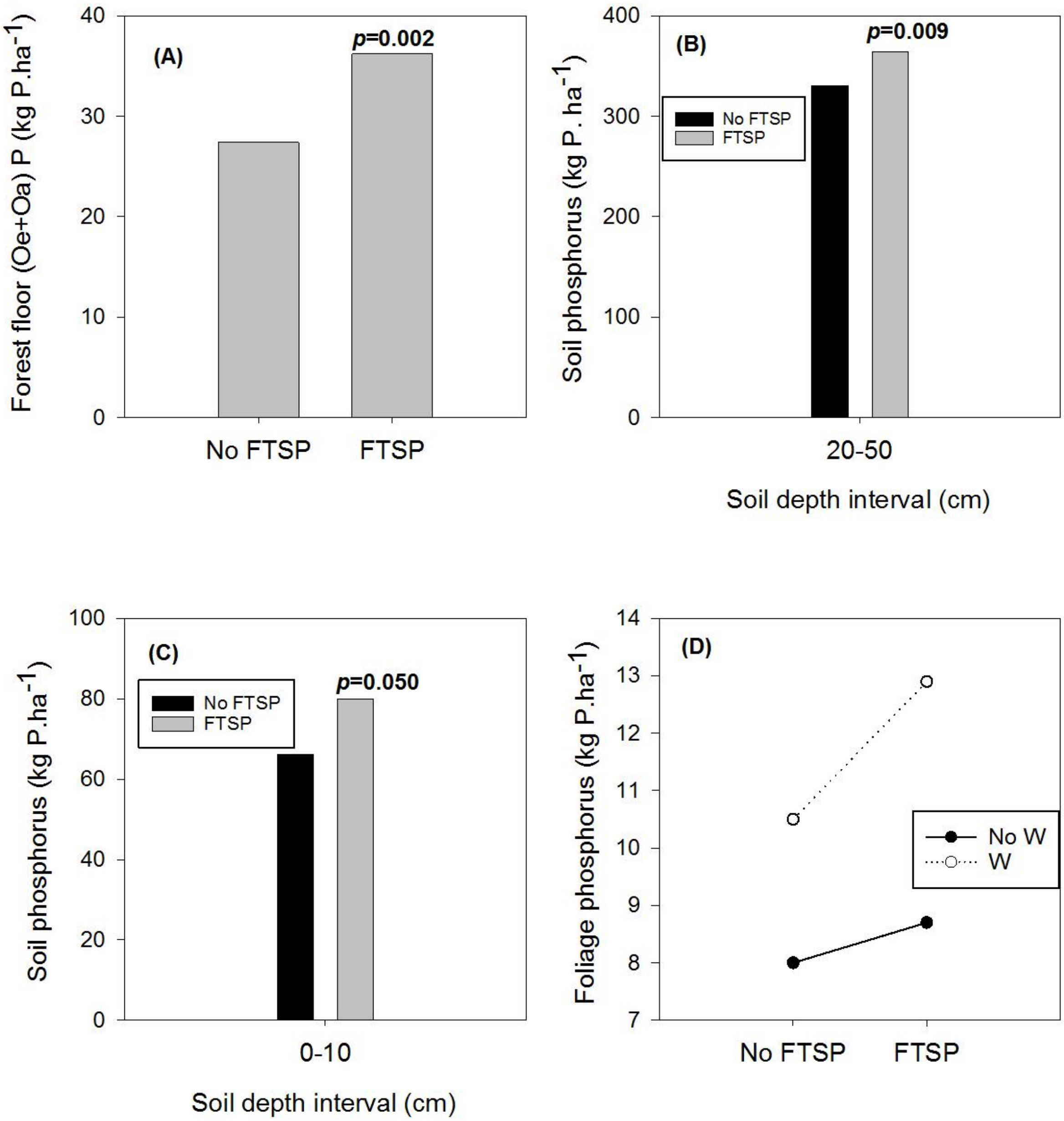

Figure 2-6. Significant F_{TSP} main effect for (A) forest floor (Oe+Oa), (B) soil (20-50cm), (C) soil (0-10cm) and F_{TSP} x W interaction effect on (D) foliage for phosphorus (P) accumulation (kg ha^{-1}) in a 25-year-old loblolly pine stand near Palatka, FL.

The F_{TSP} treatment increased P accumulation for the Oe+Oa (p=0.002) layers relative to the control treatments (Figure 2-6A). The F_{TSP} main effect was significant and resulted in an increase of P accumulation for the 20-50 cm (p=0.050) (Figure 2-6B) and 0-10 cm (p=0.009) depth intervals (Figure 2-6C). A significant interaction between F_{TSP} and W (p=0.037) highlighted that W increased foliage P when combined with F_{TSP} (Figure 2-6D).

Relative to the forest floor and vegetation pools, the soil was a much larger P pool, and had larger responses to treatment. P accumulation decreased from the 0 - 10 cm depth interval (66.2 - 126.9 Kg P ha^{-1}) to the 20 - 50 cm depth interval (46.3 - 84.6 Kg P ha^{-1}), but increased in deeper soil for the 50 - 100 cm depth interval (330.7 - 539.4 Kg P ha^{-1}) (Table A-6).

II.4.5 Plant available forms of soil N and P

Across soil depths, extractable NH_4^+ decreased from the surface to the deepest soil interval (50 - 100 cm), $NO_3^{-,}$ varied across depths and with treatment, and PO_4^{3} was greatest at the deepest depth interval. The NH_4^+ concentration decreased from the surface to the deeper soils: decreasing from the 0 - 10 cm (37.2 - 50.5 mg kg^{-1}), 10 - 20 cm (16.9 - 30.4 mg kg^{-1}), 20 - 50 cm (7.3 - 19.3 mg kg^{-1}), and the 50 - 100 cm depths (1.7 - 23.2 mg kg^{-1}) (Table A-10). Extractable NO_3^- concentrations decreased from the 0 - 10 cm (38.1 - 55.57 mg kg^{-1}) to the 10 - 20 cm (26.8 - 55.67 mg kg^{-1}) intervals except for the C and F_{TSP} treatments, then tended to increase from 20 - 50 cm (19.5 - 69.6 7 mg kg^{-1}) and to 50 - 100 cm (27.5 - 49.77 mg kg^{-1}) depth intervals. Significant NO_3^- increases first appeared in the 20 - 50 cm interval for the C, F_{DAP}, F_{DAP}W and F_{TSP}W treatments and in the 50 - 100 cm depth intervals for the F_{DAP}, W, F_{TSP} and F_{TSP} W treatments (Table A-10). Extractable phosphorus (PO_4^{3-}) concentrations were the greatest in the 50 - 100 cm depth range (4.5 - 9.7 mg kg^{-1}), followed by the 0 - 10 cm (1.3 - 3.8 mg kg^{-1}) and 10 - 20 cm (0.4 - 2.7 mg kg^{-1}) and the lowest in the 20 - 50 cm (0.1 - 0.7 mg kg^{-1}) depth intervals (Table A-10).

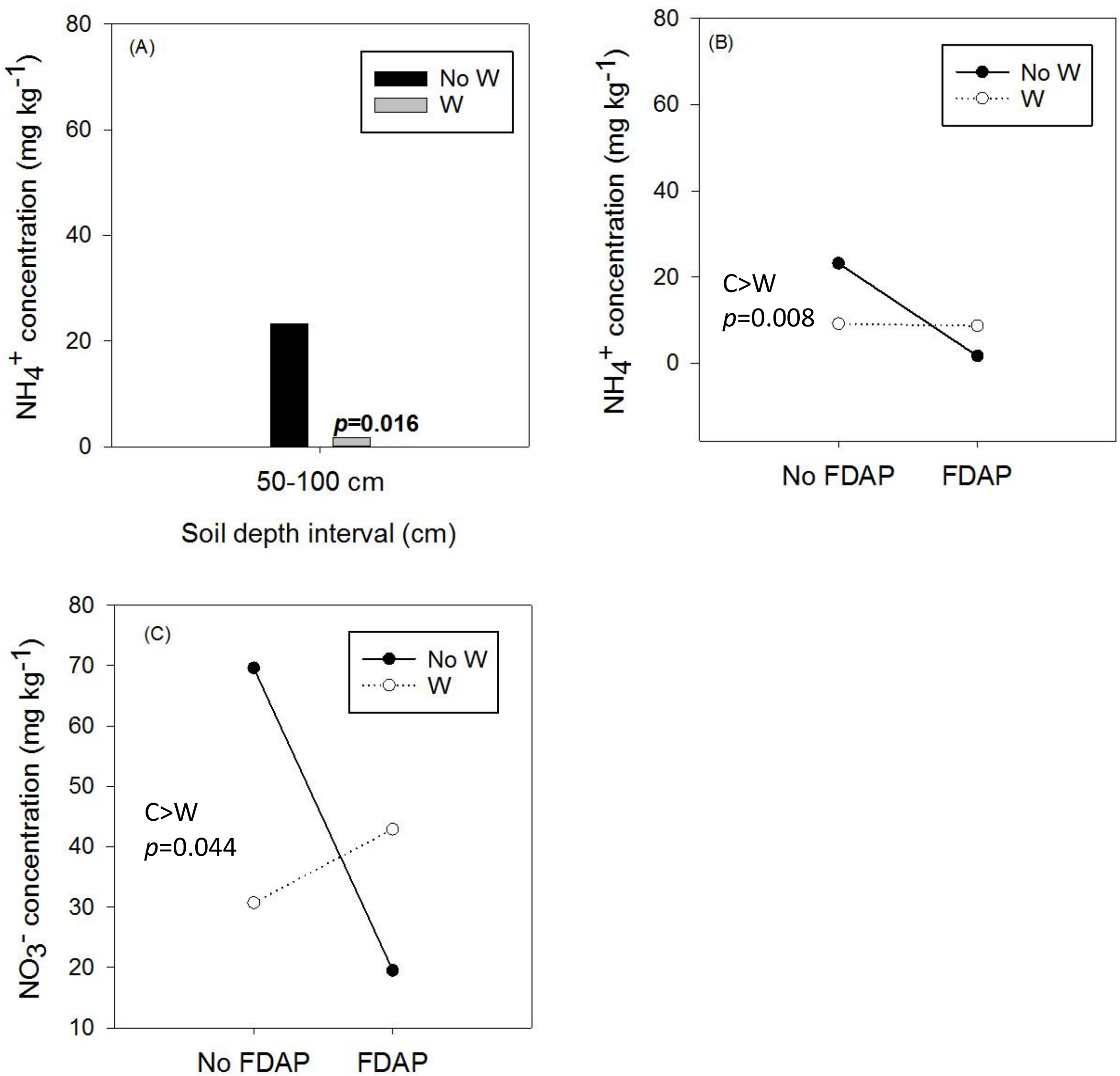

Figure 2-7. Significant main W effect for soil extractable (A) ammonium (NH_4^+) for the 50 - 100 cm depth, and F_{DAP} x W interactions for (B) NH_4^+ for the 50 - 100 cm depth, and (C) nitrate (NO_3^-) concentrations (mg kg^{-1}) in the 20 - 50 cm depth in a 25-year-old loblolly pine stand near Palatka, FL.

Soil extractable N and P showed differential response to the fertilization treatments (Table A-10). Extractable NH_4^+ did not respond significantly to either to F_{DAP} nor to F_{TSP} treatments across depth intervals (Table A-11). For the F_{DAP} treatment, the W main effect decreased extractable NH_4^+ in soil (50 - 100 cm cm) (Figure 2-7A). The F_{DAP} x W interaction effect was significant for extractable soil NH_4^+ (50 - 100 cm; *p*=0.019) (Figure 2-7B) and NO_3^- (20 - 50 cm; *p*=0.021) (Figure 2-7C); weed control alone decreased NH_4^+ and NO_3^- relative to concentrations without fertilization (C > W), but NH_4^+ was higher when weed control was combined with F_{DAP} relative to F_{DAP} alone.

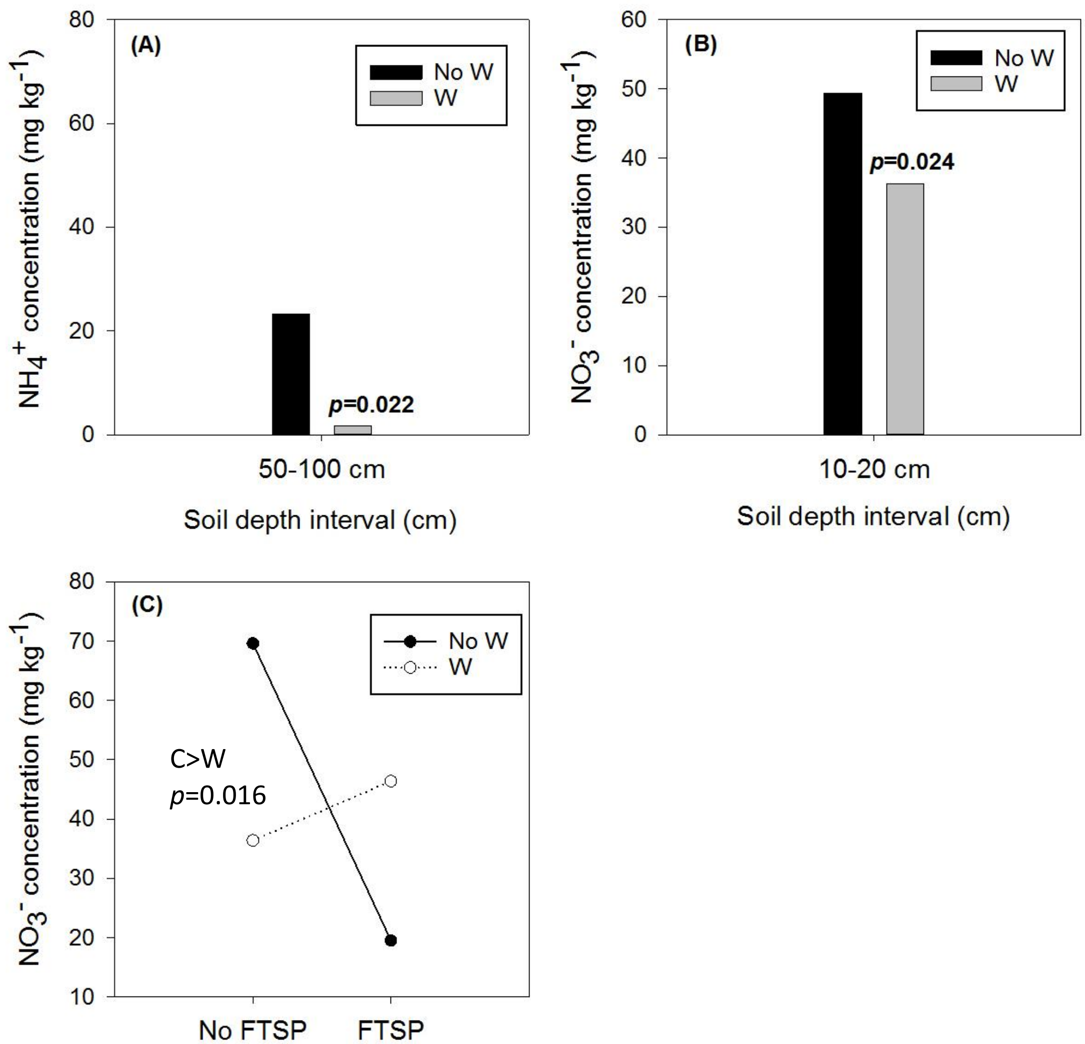

Figure 2-8. Significant W main effect for (A) soil (50 - 100 cm) on extractable ammonium (NH_4^+); W main effect for (B) soil (10-20 cm) and F_{TSP} x W interaction effect for (C) soil (20 - 50 cm) on extractable nitrate (NO_3^-) concentrations (mg kg^{-1}) in a 25-year-old loblolly pine stand near Palatka, FL.

There were significant F_{TSP} and W treatment effects on extractable N and P. For the F_{TSP} treatment, competition control decreased extractable NH_4^+ in the 50 - 100 cm (23.2 vs. 1.7 mg kg^{-1}; p=0.022) (Figure 2-8A) and NO_3^- in the 10- 20 cm (49.4 to 36.3 mg kg^{-1}; p=0.024) (Figure 2-8B). For NO_3^-, the interaction effect between F_{TSP} and W (Figure 2-8C) in the soil (20 - 50 cm depth interval) reflected that W decreased concentrations without fertilization (C > W) but increased concentrations with fertilization.

For extractable PO_4^{3-}, F_{DAP} treatment had a significant positive effect in the 0-10 cm and 50-100 cm depth intervals (Figure 2-9A). A significant F_{DAP} x W interaction effect reflected a decrease in PO_4^{3-} concentration when F_{DAP} was combined with competition control relative to F_{DAP} alone in the 10-20 cm (Figure 2-9B) and 20-50 cm (Figure 2-9C) depth intervals.

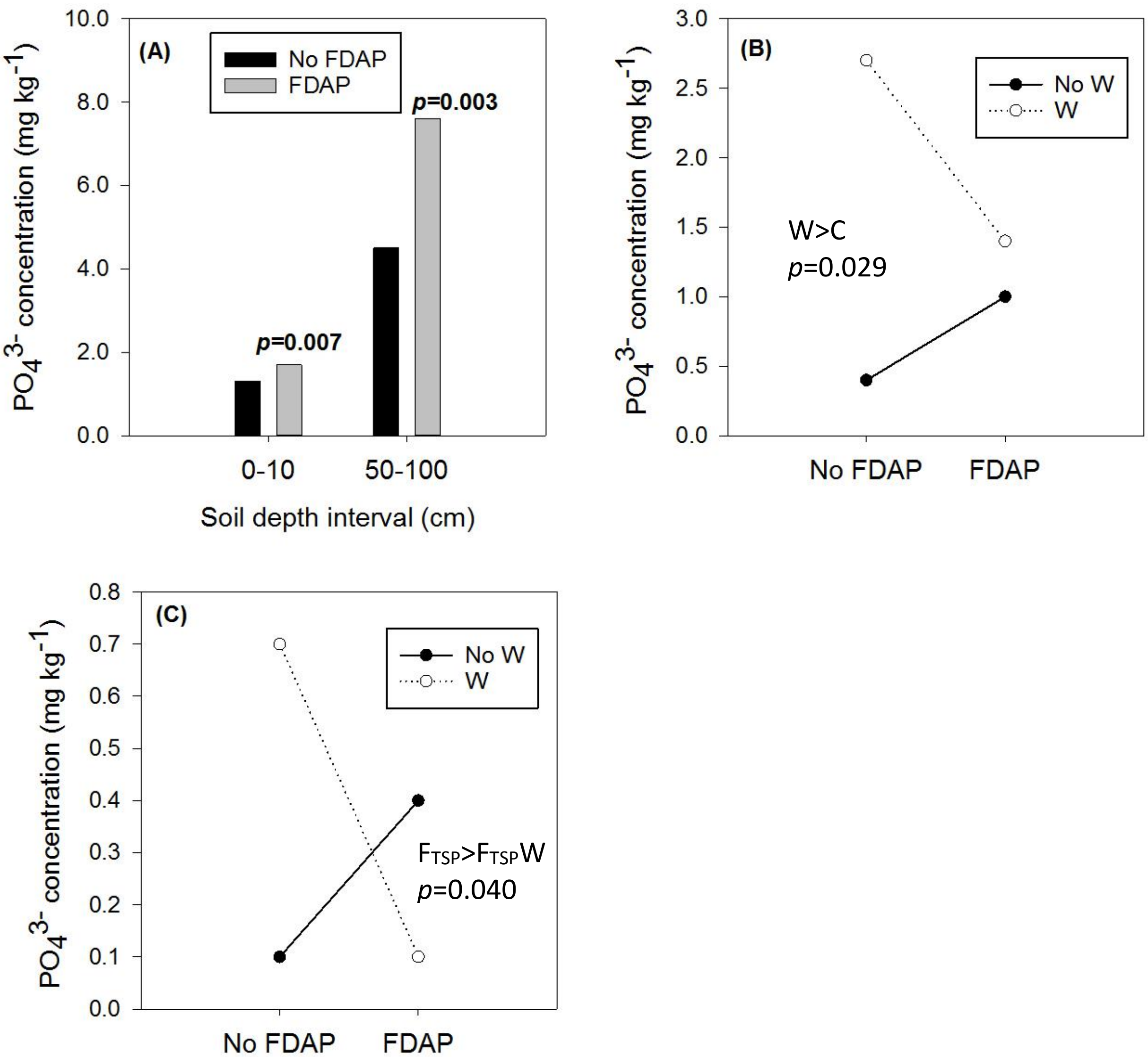

Figure 2-9. Significant F_{DAP} main effect for (A) soil (0 - 10 cm and 50-100 cm) and F_{DAP} x W interaction effect for (B) soil (10 - 20 cm) and (C) soil (20 - 50 cm) on extractable phosphorus (PO_4^{3-}) concentration (mg kg^{-1}) in a 25-year-old loblolly pine stand near Palatka, FL.

Similar to F_{DAP} treatment, F_{TSP} significantly increased extractable PO_4^{3-} in 0-10 cm and 50-100 cm depth intervals (Figure 2-10A). A significant F_{TSP} x W interaction effect reflected that extractable PO_4^{3-} was higher in 10-20 cm depth interval with F_{TSP} alone than when it was combined with competition control (Figure 2-10B).

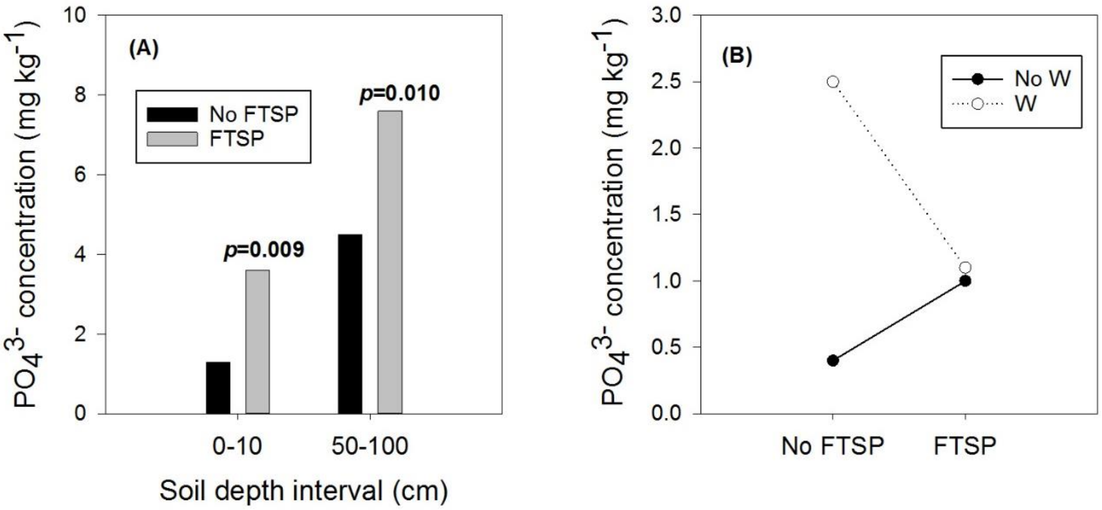

Figure 2-10. Significant F_{TSP} main effect for (A) soil (0-10 cm and 50 - 100 cm) and F_{TSP} x W interaction effect for (B) soil (10 - 20 cm) on extractable phosphorus (PO_4^{3-}) concentration (mg kg^{-1}) in a 25-year-old loblolly pine stand near Palatka, FL.

II.5. Discussion

The limitations to pine productivity in the southeastern United States can affect the region's economy and the C sequestration of plantations (Han et al. 2007). This study's objective was to assess these limitations by examining how ecosystem C, N, and P dynamics responded to forest management practices. In general, the productivity of pine plantations in the region are co-limited by N and P (Fox et al. 2007a), so one would expect fertilization with N and P to increase ecosystem C accumulation. However, at this study site the addition of N and P fertilizer alone did not increase pine biomass or ecosystem C accumulation and only its combination with weed control produced a modest biomass effect (Figure 2-1B; Table 2-2). A likely contributor to this non-response to fertilization-only treatments was that this site was inherently very productive, as the control had a site index of 27.0 m (Table 2-3), making it one of the more productive untreated pine plantations in the southeastern United States (Sabatia and Burkhart 2014). Along gradients in fertility, the fertilization of increasingly productive sites results in decreasing fertilization benefits in pine growth (Carlson et al. 2014). The observation here that this result also translates to little change in ecosystem C accumulation suggests that a management type (e.g. fertilization) may not uniformly increase ecosystem C accumulation across sites that vary in native fertility. In a study similar to this one but on a much less productive site (site index = 19.5 m) (Jokela et al. 2010), a high level of fertilization with both micro- and macronutrients significantly increased tree plus organic soil C accumulation by ~45% (Vogel and Jokela 2011). These results suggest that increasing C accumulation requires a growth response in the pine trees, and in the case of fertilization, this growth response will decrease with an increase in background fertility.

The increases in biomass C accumulation that occurred when fertilization was combined with competition control began as a strong early positive effect that carried through to the end of rotation (Figure 2-1, 2-2). Competition control and fertilization are often additive in their effects on pine growth (Jokela et al. 2010), and in an analysis of 10 experimental sites aged 5-8 years (including this one), loblolly pine stand growth at all sites responded significantly to fertilization combined with competition control (Jokela et al. 2000). In this study, part of the stand growth response in the combined treatments was due to greater pine survivorship with competition control, a common phenomenon in southern pine plantations (Haywood and Tiarks 1990). Moreover, individual tree growth was also increased by the combined treatments (Jokela et al. 2000) suggesting that the presence of the understory created a limitation to growth. Understory plants in these plantations can accumulate relatively large amounts of micro- and macronutrients (Subedi et al. 2014), which were not added in the fertilizer mix at G8 (other than Ca). Notably, micro- and macronutrients have been shown to limit pine productivity in other Florida Spodosols (Jokela et al. 1991, Vogel and Jokela 2011).

The dynamics of ecosystem C pools often strongly correlate with changes in nutrient pools (Harding and Jokela 1994, Vogel et al. 2011), and nutrient pool changes could indicate changes in site productivity and whether management practices are sustainable, or whether productivity levels can continue into the future (Kiser and Fox 2012). In the current study, N and P pools in pine biomass generally followed biomass C, reflecting the trend of fertilization interacting with competition control. Fertilization did increase N and P in some pools, a result that agrees with previous findings of increases in soil and forest floor N (Johnson et al. 2003, Will et al. 2006, Vogel et al. 2011) and P (Polglase et al. 1992b, Grierson et al. 1999) with fertilization in loblolly pine and slash pine plantations in the southeastern United States. In contrast, the W effect significantly decreased the P forest floor pool suggesting this element may be less available in the next rotation. A reduction in next rotation growth in W-only treatments relative to a control was previously reported by Subedi et al. (2014), suggesting that this treatment applied by itself could lead to a reduction in potential site productivity.

One-time extractions provide only a partial expression of nutrient availability, but they are often used for evaluation of site fertility in plantation systems (Comerford and Fisher 1982). For extractable N and P, fertilization increased PO_4^{3-} consistently across soil horizons. However, for N, the effects of W decreased both NH_4^+ and NO_3^- relative to the control plots, but often increased them where fertilizer was also applied. These differences among N and P response may be related to variation in litter chemistry (Polglase et al. 1992b), because in the W treatments the litter would have derived nearly entirely from pine tissues, while the fertilized-only and control plots would have more tissues deposited from woody and herbaceous understory plants. The only metric of organic matter chemistry for these experiments are the C: N or C: P ratios, but these do not show clear trends or differences (not shown) that would identify reasons for the differences in extractable nutrients. Without additional information on organic matter chemistry or microbial function, the underlying reasons for the differences between N and P in extractable elements are difficult to explain, but highlight how silvicultural practices can change these metrics of site productivity.

The results from both the pools and extractions suggest that the treatments had some significant effects throughout the soil profile, pointing to the potential for high levels of nutrient movement. The pools of P tracked via extractable PO_4^{3-} for the fertilization treatments suggest some fertilizer P moved downward in the soil profile. Similar evidence for downward movement for N with fertilization was also found for N pools, although the results for extractions were unclear on whether there was a fertilization effect. Whether these movements reflect potential fertilizer nutrient losses and export to water bodies from the system is also uncertain, in particular, because our 1-meter sampling depth did not capture the argillic horizon that is typical of the Pomona soil series. This more clayey horizon likely has greater exchange capacity and potential to capture N and P (Piatek and Allen 2001, Kissel et al. 2009, Zerpa and Fox 2011). Another point of potential nutrient capture, the spodic horizon was found at the transition between the 20-50 cm and 50-100 cm depth intervals, but its ability to bind P with organic matter depends on the concentration and activity of Al and Fe sesquioxides (Walker and Syers 1976, Gallardo and Schlesinger 1994, Kiser and Fox 2012) that are dominant in this horizon. A critical question is whether this exchangeable pool of P deep in the soil profile will be available to future trees as roots grow into the deeper soil layers. A study on a nearby Spodosol found PO_4^{3-} concentrations to be greater at soil depths >20 cm both in the spodic and argillic horizons after past fertilization and fertilization plus competition control treatments (Subedi et al. 2014), suggesting P retention is occurring throughout the soil profile.

II.6. Conclusions

Silvicultural treatments had only modest effects on C pools at this site, but both the N and P pools responded to fertilization and to a lesser degree competition control. The relatively muted response of tree productivity to fertilization likely reflected the high background soil fertility and site quality. This observation could be representative of a general phenomenon, as fertilization effects on pine growth are known to diminish with increased site fertility. A key unknown is whether the increases in nutrient pools in the forest floor and soil that occurred with fertilization, or reductions with competition control, could affect pine growth potential in the next rotation. Forest managers could adjust fertilization rates with improved knowledge on the influence of these nutrient pool changes across rotations.

CHAPTER III

CARRY-OVER EFFECTS OF FERTILIZATION AND WEED CONTROL ON TREE GROWTH AND SOIL NUTRIENT DYNAMICS IN A LOBLOLLY PINE PLANTATION IN NORTH CENTRAL FLORIDA

III.1. Synopsis

An inter-rotational experiment was established on a Spodosol in north central Florida to understand the effect of intensive silvicultural practices on the sustainability of repeatedly growing loblolly pine *(Pinus taeda* L.) plantations on the same land base. Fertilization and competition control treatments used in the first rotation were evaluated for their effect on next-rotation tree growth. Soil C and N concentrations, concentrations of plant-available forms of N and P, and potential mineralization rates obtained from soils collected at age 2 years were used to understand how past silvicultural treatments affected soil nutrient supply. The first rotation experiment consisted of a complete randomized block design having a control (C), two types of fertilization (F), competition or 'weed' control (W), and two types of fertilizer plus weed control (FW) treatments. In the second rotation, untreated carry-over (C-) plots (CC, CF, CW, and CFW) were created for one fertilizer type to evaluate relative sustainability, while the other fertilizer plots were retreated (R-) with fertilizer (RF) and fertilization plus competition control (RFW). At three years of age the second rotation height growth ranged from 3.2 m in the CW up to 4.6 m in the RFW, and exceeded the first rotation from a minimum of 2.3x (FW→RFW) up to a maximum of 3.4x (C→CC). Stand biomass ranged from 5.9 Mg ha^{-1} (CW) to 17.9 Mg ha^{-1} (RFW) at age four years, with pair-wise comparisons showing the RFW significantly ($p<0.05$) greater than all other treatments and the RF exceeding the carry-over treatments. For average tree diameter at breast height

(DBH), the CW tree's DBH of 5.5 cm was significantly less than all other treatments (range 6.1-8.9 cm), the RF and RFW were greater than all carry-over treatments, and the CF was greater than the control. Changes in available nutrients mirrored the carry-over growth trends, as the CW treatment initially reduced extractable NH_4^+, while the CF treatment increased extractable PO_4^{3-}. Whether these soil responses will result in persistent growth change is unclear, because CW also increased soil C, C: N ratio, and net N mineralization, suggesting that N availability could eventually increase over time. For CF, the lack of change in N pool sizes or mineralization could lead to eventual N limitation. The dramatic increase in productivity across rotations and the responses to retreatment were both much greater than carryover effects, highlighting that there is likely to be continued increases in productivity regardless of past silviculture.

III.2. Introduction

In tree plantations worldwide, fertilization and competition control through herbicide application are commonly used to accentuate tree growth (Reed 1978, Wernick et al. 1997, Perry 1998, Lautenschlager 2000, Wu et al. 2011, Zhao et al. 2013) by reducing intra- and interspecies competition for limiting soil resources (Harper 1977, Stewart et al. 1984, Nambiar and Sands 1993, Wagner et al. 2006, Mangla et al. 2011). In the southeastern United States, both treatments have contributed to a 3-4 fold increases in pine productivity over the last several decades (Allen et al. 1990, Colbert et al. 1990, Neary et al. 1990, Jokela and Martin 2000, Fox et al. 2007b), and are now a commonplace practice, often in combined applications (Neary et al. 1990, Jokela and Martin 2000, Borders et al. 2004, Straka et al. 2005, Miller et al. 2006, Jokela et al. 2010). With interest in ensuring forestry practices are sustainable and efficient, researchers have examined the potential for these practices to alter long-term site productivity through changes in site nutrient availability

(Dyck and Cole 1994, Morris and Miller 1994, Powers et al. 2005, Gonçalves et al. 2008, Dyck et al. 2012).

Changes in plantation nutrient dynamics can be either from a direct change from fertilization, or indirect changes from competition control (Vogel et al. 2011). N and P are generally accepted to be limiting nutrients to ecosystem productivity (Vitousek et al. 2010), and in the pine plantations of the southeastern United States, both are widely applied as fertilizer (Fox et al. 2007a). Given the differences in how the two elements cycle, it is likely that they will have different effects on long-term productivity (Pritchett and Comerford 1982, Kimmins 1996, Fox et al. 2011, Kiser and Fox 2012). For competition control, removing aboveground vegetation without returning nutrients as fertilizer could result in decreased nutrient availability in the subsequent rotations (Powers et al. 1990).

Fertilization with P can increase long-term site productivity (Walker and Syers 1976, Pritchett and Comerford 1982, Harding and Jokela 1994, Comerford et al. 2002, Subedi et al. 2014) when the P is retained in mineral soil by Al and Fe-oxides (Yuan et al. 1960) or organic P, resulting in sustained, elevated, soil P availability (Ballard 1978, Pritchett and Comerford 1982, Everett and Palm-Leis 2009, Fox et al. 2011). In a study conducted on P deficient soils both in Georgia and New Zealand, Comerford et al. (2002) documented a significant effect of P fertilization that was observed both in the forest floor and mineral soil 29 and 22 years after fertilization at the above sites, respectively. Gentle et al. (1986) reported elevated levels of available P and a continued growth response in subsequent rotations, demonstrating a long-term increase in soil quality. Relative to P, the N outputs are more varied and dynamic with losses as gaseous N, and N also has greater leaching potential as an anion because its soil retention is often weaker than P. Inputs of N are also varied, with N_2 fixation and deposition continuously adding N to the ecosystem. With the large natural exchanges of N, fertilization with this element may have less of an effect on long-term productivity than does P fertilization. However, early after harvest the N in plant tissues or soil organic matter may become available to plants during microbial mineralization, a process called the Assart effect (Kirnmins 1997).

Changes in site productivity may co-occur with changes in N and P pool sizes and mineralization rates. Site productivity could increase in the next rotation if fertilizer is retained in the soil, which often occurs in pine plantations. For example, Will et al. (2006) estimated that ~90% of applied N as inorganic fertilizer was retained, while in excess of 100% of the added P was retained in a loblolly pine plantation. N and P fertilizer retention has varied with whether competition control occurred with the fertilization. Vogel et al. (2011) estimated that 103% and 63% of the applied N was retained in fertilized plots of loblolly pine and slash pine plantations, respectively in north-central Florida, but the amount decreased when weed control was performed with fertilization by 41% for loblolly pine and 10% for slash pine. Sustained increases in rates of nutrient cycling and mineralization following fertilization have been documented (Maimone et al. 1991, Dalla-Tea and Jokela 1994), but for competition control, decreases in inorganic N (Rifai et al. 2010) and P (Polglase et al. 1992b) have been observed. Although there is some evidence that this translates into lower production early in the next rotation, the effect seems to be transitory and could be related changes in understory competition (Subedi et al. 2014).

The overall objective of this study was to determine the carry-over effects of fertilization and competition control, applied in the previous rotation, on the next rotation's growth and nutrient dynamics. Previously, I reported that at this site in north central Florida, the forest floor and extractable N and P pools increased with fertilization, while competition control combined with fertilization increased nutrients in vegetation at the end of a 25 year rotation (Chapter II). Here I determined tree growth for the first four years after planting, and the soil C and N pools and N and P mineralization. I hypothesized that treatments used in the first rotation would have residual effects on the next rotation's early soil nutrient dynamics, with the directional changes in pine growth predicted by changes in nutrient dynamics.

III.3. Material and methods

III.3.1 Site description

The research area was originally one of 25 'G-series' experimental sites that were established in 1987 by University of Florida's Cooperative Research in Forest Fertilization in partnership with the Auburn University Silviculture Herbicide Cooperative. The overall study's goal was to evaluate the effect of fertilizer, competition control and the combined treatments on the potential growth of managed pine forests (Jokela and Martin 2000). The study site, called 'G8', was located near the city of Palatka, FL (29°38′N, 81°39′W). Upon completion of the G8 study, an evaluation of C, N, and P pools and extractable nutrients was conducted (Chapter II). A new study was established in 2013, entitled the Silvicultural Sustainable Productivity Study (SSPS), which was used to understand the "carry over" effects of the first rotation's silvicultural treatments on the second rotation's pine forest production and nutrient dynamics. Retreatment with fertilization and competition control on some plots was used to estimate full site growth potential.

The nearby city of Palatka receives mean annual precipitation of 1279 mm and has a mean annual temperature of 21.2 °C (NOAA, 1984- 2013). The climate of the site is sub-tropical (i.e. warm and humid). The soils of the site are mapped as poorly drained Spodosols, and at this site by the Pomona soil series (sandy, siliceous, hyperthermic Ultic Alaquods) and it is acidic soil (pH=4-5). Soil texture specifically for this site was estimated using the hydrometer method as ~83% sand, 11% silt and 6% clay in the upper 1-m. The spodic horizon generally occurred between 60 and 80 cm depth, and an argillic horizon at approximately 1.2 m (Vogel, personal observation). The elevation of the site is 5 m, it has ~1° slope in a westerly direction from its center. It is located approximately 280 m from a nearby stream (Rice Creek).

III.3.2 Study Design and Treatments

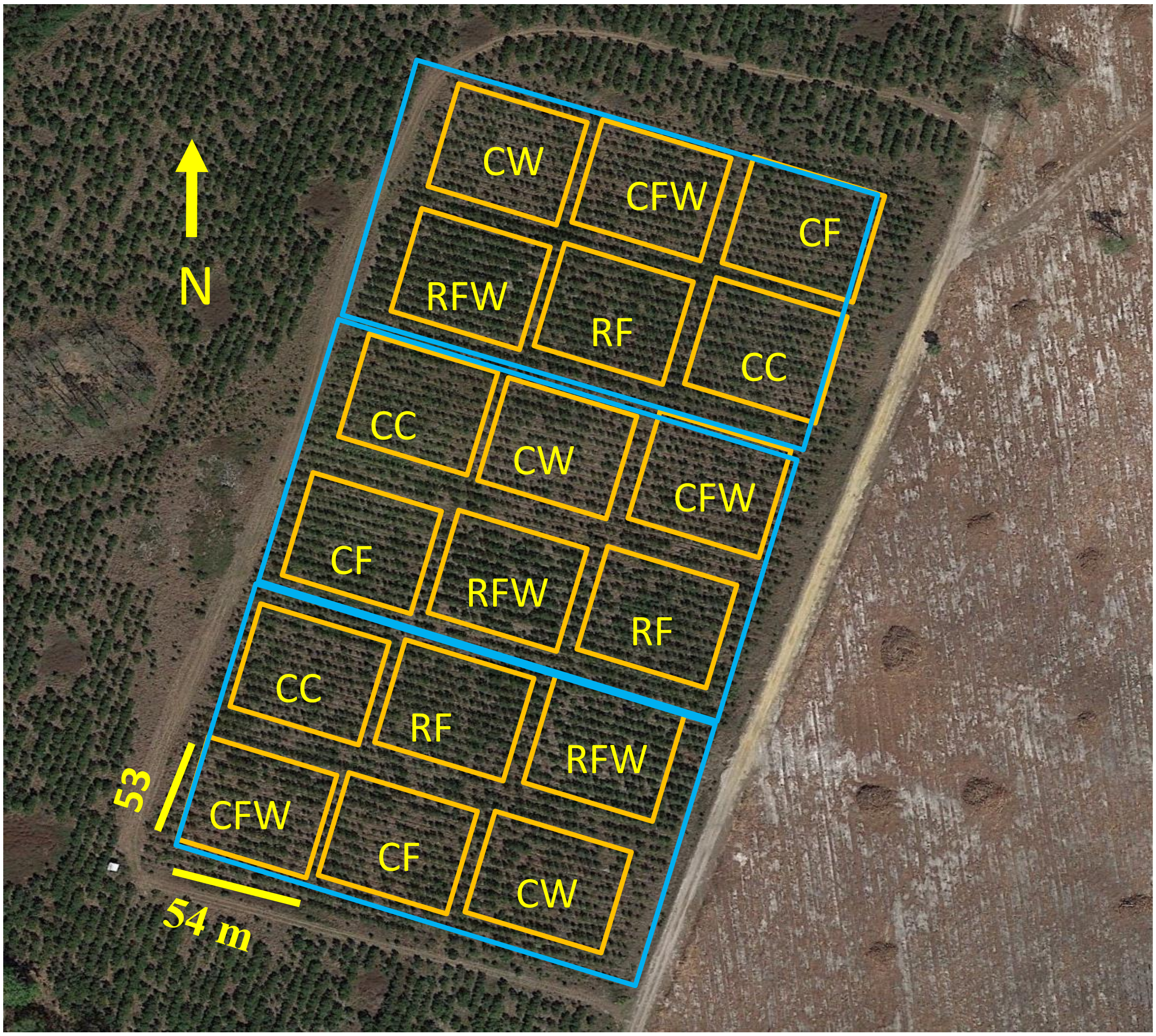

Figure 3-1. SSPS experiment and treatments

The new SSPS experiment (Figure 3-1) was established on the previously harvested G8 experiment, which was originally a randomized complete block design (RCBD). Previously, the three blocks had six treatments: Control (C), fertilization with diammonium phosphate (DAP) or triple superphosphate (TSP) (F), competition or 'weed' control (W), and fertilization with either DAP or TSP and competition control (FW). The fertilization amounts (~280 kg N, 100 kg P), timing of application, and herbicides used in the 1st rotation are detailed in Chapter II. The carry-over experiment was on the control (CC), competition control (CW), and the previously fertilized DAP plots (CF, CFW). Retreated plots (RF, RFW) received fertilizer either alone or in combination with competition control treatments (Table 3-1). All plots were double pass bedded with the first pass occurring in April 2012 and the second in September 2012. Planting occurred in January of 2013, using a single full-sib family of second generation containerized seedlings. Seedling were mass control-pollinated loblolly pine with an eastern range provenance. It was the same family as planted in Subedi et al. (2014), and seedlings were planted at 2.2 m x 3.0 m spacing. To ensure the establishment of pine, herbaceous species, primarily *Panicum* spp., were controlled with an herbicide (hexazinone and sulfometuron methyl, Oustar™) sprayed in bands on all beds in April 2013. Fertilizer included N, P and K and micronutrients (Mn, Cu, Fe, Zn and B) and the RFW treatment received multiple applications of herbicide (Table 3-1).

Table 3-1. Fertilizer application rates (kg ha^{-1}) and competition control for retreated fertilized-only (RF) and combined treatments (RFW) for a loblolly pine plantation in its second rotation. Untreated carryover (CC, CF, CW, CF) plots are described in the text.

Treatment	Fertilization	Weed Control
RF	56 N, 2.2 P, 47 K, 0.616 Mn, 0.224 Cu, 1.456 Fe, 0.560 Zn, 0.224 B	None
RFW	56 N, 2.2 P, 47 K 0.616 Mn, 0.224 Cu, 1.456 Fe, 0.560 Zn, 0.224 B	Broadcast Chopper 3.2 kg/ha prior to planting and again after 1 year. Repeat directed spot spray with glyphosphate through age 2.

III.3.3 Tree Measurements

Tree height (m) was measured every year after planting for the first four years and diameter at breast height (DBH; cm) was measured on all trees in the fourth year. To contrast the first and second rotation, tree heights were used because these were measured for ages 2 and 3 years in both rotations. To estimate the carry-over effects of the first rotation's silvicultural treatments on the second rotation's growth, the fourth year's heights and DBH were used to estimate tree biomass. DBH was used to contrast average tree size at age 4.

III.3.4 Soil sampling and analysis

Two years after planting (January, 2015), the mineral soil samples were collected at depth intervals of 0-10 cm, 10-20 cm, and 20-50 cm using a 7.62 cm diameter soil auger. Soil sampling was stopped at 20-50 cm depth because the deeper soils were excessively wet due to a high-water table and the soil could not be removed. Soils were collected in each treatment plot with three each from the bed and inter-bed areas. The samples were thoroughly mixed by plot, depth and location (bed or interbed) to make a composite sample. Approximately 1000 g was removed for subsequent analysis. These samples were weighed wet and stored at 4˚C until analyzed. The soil was passed through a 2 mm sieve and roots and large wood fragments were removed from the top of the sieve and weighed. Approximately 10% of the soil mass was oven-dried at 65 ˚C, and then ground on a roller ball mill for 48 hours until fully pulverized. The soil C and N concentrations were analyzed by dry combustion using an elemental analyzer (Thermo Finnigan FLASH EA 1112). The standard soil N C reference material was used to assess the accuracy of the C and N measurements. This material consisted of purified and homogeneous lot of soil NC used in the calibration of elemental analyzers for determination of C and N concentrations. For mineral soils, carbonate removal via acidification was not performed because the low pH (4-5) and highly weathered nature of the soils precluded the presence of carbonates. Because the bedding disturbed and mixed the soil matrix with detritus, bulk density was not estimated and C and N are reported as concentrations.

Relative differences in N and P availability were estimated using both an initial extraction and the amount of N and P mineralization after an 11- month laboratory incubation. Immediately prior to placing a soil sample in a 20 ml scintillation vial, a 1 M KCl solution was used to extract NO_3^- and NH_4^+ (Keeney and Nelson 1982) and Mehlich III solution (0.2 M CH_3COOH+0.25 M NH_4NO_3+0.015 M NH_4F+0.013 M HNO_3+0.001 M EDTA) was used as an extract for available P

(PO_4^{3-}) (Mehlich 1984). For the KCl extract, 3.0 g of soil was mixed with 30 ml of 1.0 M KCl extracting solution (soil: solution ratio 1:10) and placed on a shaker for 30 minutes (120 oscillation/minute). For the Mehlich III extract, about 3.0 g of soil was mixed with Mehlich III extracting solution (soil: solution ratio 1:10) and placed on a shaker for 5 minutes (120 oscillations/minute). Extracts were filtered through pre-rinsed Q2 filter papers into scintillation vials and frozen until chemical analyses were performed. Different chemical reactants were added to the samples that changed the colors of solutions. Salicylate and bleach solutions, Vanadium cocktail solution and Malachite Green solution were added to $NH4^+$, NO_3^- PO_4^{3-} samples, respectively. Solution color was blue green for NH_4^+, pale to bright pink for NO_3^- and green for PO_4^{3-} and were read at read at different wavelengths: 650 nm, 540 nm and 630 nm, respectively using the colorimetric method with a spectrophotometer EON Microplate reader (Biotek Instruments, Inc.). Prior to measurements, Ammonium standard, Nitrate standard and 1,000 ppm phosphorus AA standard were used to assess the accuracy for $NH4^+$, NO_3^- and green for PO_4^{3-}, respectively. For the incubation, soil moisture was brought to near field capacity and incubated on the benchtop at room temperatures (~22°C-25°C).

The soil texture for each soil interval was analyzed using the Bouyoucos hydrometer method (Bouyoucos 1962). Briefly, 50 g of oven-dried at 65 °C soil that passed through a 2 mm sieve was mixed with a dispersing agent (2.5 N sodium hexametaphosphate, $(NaPO_30)_6$) and deionized water. A calibrated hydrometer was inserted into the suspended materials for 40 seconds and the hydrometer reading gives the amount of suspended silt and clay particles per liter while the sand particles are settled at the bottom of the cylinder. After 2 hours settling, another hydrometer reading was recorded that gives the amount of suspended clay particles per litter. The sand fraction was calculated based on the amount of clay and silt in a sample. The hydrometer readings were corrected according to the temperatures measured at both readings.

III.3.5 Statistical analyses

Data for the carry-over treatments were analyzed as a randomized complete block experimental design (RCBD) analysis of variance (ANOVA) using the SAS PROC MIXED modeling procedure (Littell et al. 1998) (SAS Institute Inc., 1988). The differential carry-over effects of treatments were determined for the response variables, tree growth, soil C and N concentrations, and N and P extractions and mineralization, with the main effects of fertilization, competition control, depth and location (bed vs. interbed) and all possible interactions. Treatments (T), location (L), and depth (D), were treated as fixed effects while blocks were treated as random effects. For tree growth, average individual DBH and stand biomass were analyzed for the latest measurement (age 4 years) and a pairwise comparison was conducted on all treatments. Tukey's studentized range (HSD) test was used to separate treatment means ($\alpha < 0.05$).

III.4. Results

III.4.1 Inter-rotational comparison of effect of treatments on tree growth for a loblolly pine plantation

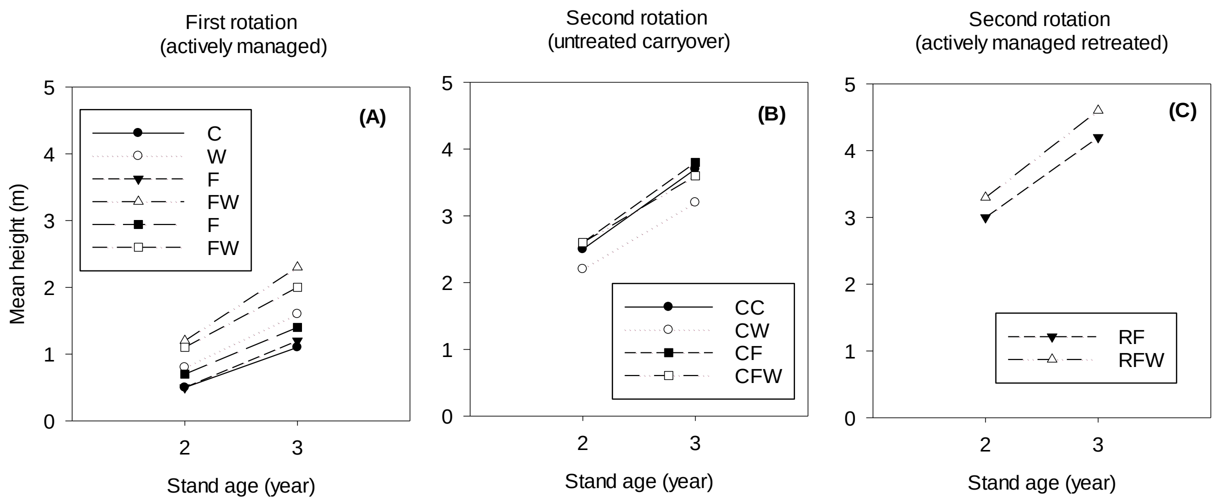

Figure 3-2. Heights for overlapping aged (second and third year) trees of (A) the first rotation study with control (C), fertilization (F), weed control (W) and their combination (FW) treatments for two types of fertilizer (triangles, squares) and (B) the second rotation untreated carry-over (CC, CW, CF, CFW) treatments and (C) the actively managed, retreated (RF, RFW) treatment for a loblolly pine plantation near Palatka, FL.

Height growth in the first rotation reached 0.5 - 1.2 m in the first year, and at age 2-years, ranged from 0.9 - 2.2 m (Figure 3-1A), with FW treatments being the only treatments significantly greater ($p<0.05$) than C. In the second rotation, height growth ranged from 2.2 m (CW) at age 2-years up to 4.6 m (RFW) at age 3-years (Figure 3-1B-C). The inter-rotational increase in height growth translated to a maximum second year to first year height ratio of 2.2x (F→CF) greater growth in year 2, and a minimum of 1.4x (FW→CFW) greater growth in year 3 (Figure 3-1A-B). In the second rotation, the RF and RFW treatments had significantly ($p<0.05$) greater heights than the control (CC), and the RFW treatment had greater ($p<0.05$) heights than RF in both years (Figure 3-1B-C).

The most recent measurements at age 4-years demonstrated the positive effects of repeated fertilization and competition control on forest biomass and average tree size, and that carry-over effects from past treatments moderated growth (Figure 3-2). Accumulating 17.9 Mg ha^{-1}, the RFW treatment grew significantly more stand biomass than any other treatment (Figure 3-2). The only other significant contrast for biomass was where the RF treatment grew significantly more than the CF treatment (Figure 3-2). Analysis of average individual tree DBH revealed a larger number of significant contrasts (Figure 3-3), with CW significantly less than all other treatments. First rotation fertilization (CF) significantly ($p=0.047$) increased DBH relative to CC, with the CFW not different from the CF and CC treatments. The RF and RFW treatments supported significantly larger average trees than all carry-over plots, and RFW had larger diameter trees than the RF plots (Figure 3-3).

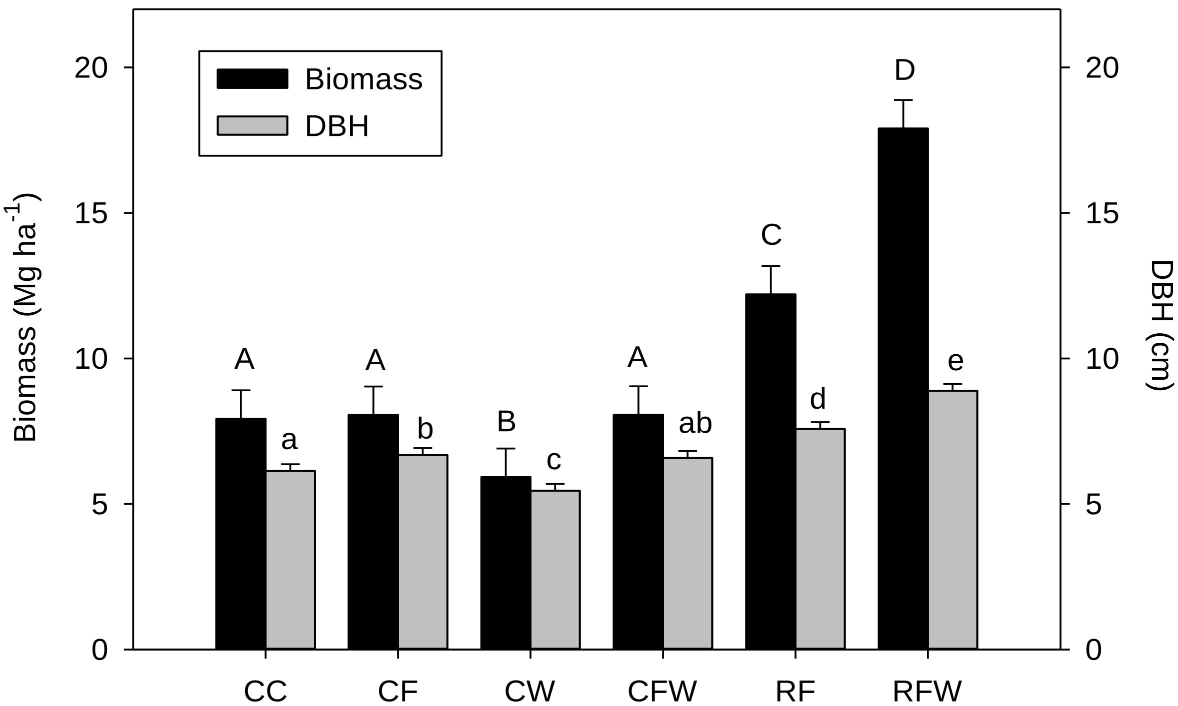

Figure 3-3. Contrasts among both silvicultural carryover (CC, CF, CW, CFW) and retreated (RF, RFW) treatments for stand biomass (Mg ha^{-1}) and average tree diameter (DBH; cm $tree^{-1}$) for the second rotation of a loblolly pine (*Pinus taeda*) plantation near Palatka, FL. Letters denote significant differences for stand biomass (uppercase) and DBH (lowercase). Numerator degrees of freedom (DF) =5 for both biomass and DBH; denominator DF=12 for biomass and DF=25 for DBH.

III.4.3 Soil Carbon concentration

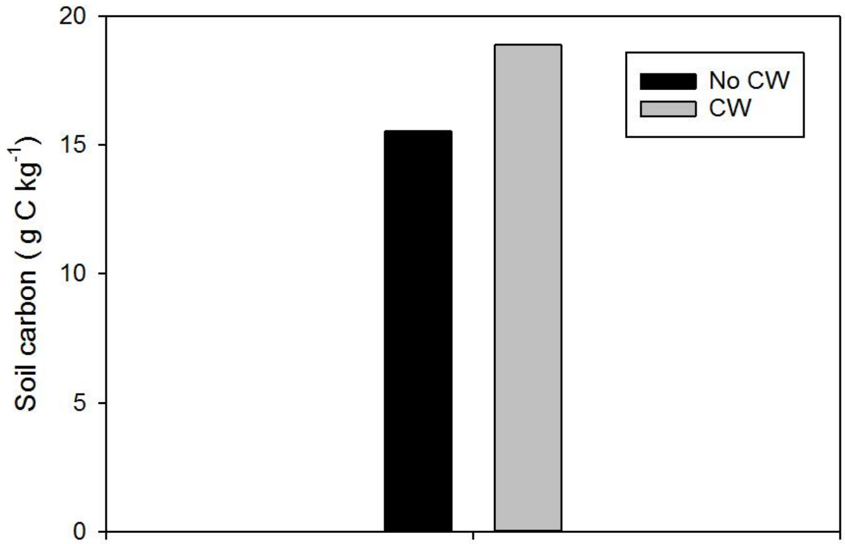

Figure 3-4. Significant CW main effect on soil C concentration for a 3-year-old loblolly pine (Pinus taeda) plantation near Palatka, FL.

Soil C concentrations ranged from 25.1 - 33.9 g kg^{-1} in the 0-10 cm, 21.5 - 28.3 g kg^{-1} in the 10 - 20 cm and 6.4 - 12.5 g kg^{-1} in the 20 - 50 cm intervals, and for the interbed C concentration ranged from 23.1 - 33.2 g kg^{-1} in the 0 - 10 cm, 10.3 - 17.0 g kg^{-1} in 10 - 20 cm, and 2.1 - 3.6 g kg^{-1} in 20 - 50 cm increments (Table B-1). The CW main effect was significant (Table 3-2), reflecting that the past competition control treatment caused an increase in C concentration of 22% relative to CC treatment probably due to dead roots (Figure 3-4). The L×D interaction was significant (Table 3-2), because the 0 - 10 cm layer of the interbed had a similar C concentration to the bed location, but C concentration decreased more with depth for the interbed position (Table B-1).

Table 3-2. Statistical summary (ρ-values) of carry-over effect from first rotation treatments of fertilization (CF), weed control (CW), and their combination (CFW) on C and N concentrations and C: N ratios for soil depths (0 - 10 cm, 10 - 20 cm and 20 - 50 cm) of bed and interbed locations of an untreated 3-year-old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

Effect	**DF**	**C**	**N**	**C: N**
CF	1	0.489	0.281	0.986
CW	1	**0.030**	0.115	**0.0002**
Location (L)	1	**0.004**	**0.007**	**0.036**
Depth (D)	2	**<.0001**	**<.0001**	**<.0001**
CF x CW	1	0.122	0.258	0.050
CF x L	1	0.242	0.260	0.197
CW x L	1	0.934	0.925	0.497
CF x CW x L	1	0.900	0.912	0.981
CF x D	2	0.668	0.699	0.603
CW x D	2	0.184	0.242	0.130
CF x CW x D	2	0.957	0.928	0.667
L x D	2	**0.003**	**0.002**	**0.035**
CF x L x D	2	0.303	0.445	0.804
CW x L x D	2	0.864	0.934	0.991
CF x CW x L x D	2	0.747	0.858	0.289

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05)

III.4.4 Soil nitrogen concentration

Soil N concentration ranged from 0.87 to 1.1 g kg^{-1} in the surface 0 - 10 cm layer, and decreased down to the 20 - 50 cm layer, ranging 0.30 to 0.90 g kg^{-1} (Table B-4). In general, it followed the vertical and location trends found for C concentration, with a significant L×D interaction (Table 3-2). For both locations there was a significant decrease in N concentration with depth (Table 3-2), and the bed tended to have greater N concentrations in the two deeper depths across treatments. The CW treatment tended to have greater N concentration (14% greater), which was similar to the increase observed for the C concentration, but it was not significant (ρ=0.115, Table 3-2).

III.4.5 Soil C: N ratio

Similar to C concentration, a significant L×D interaction was observed for the C: N ratio and the main effect of the CW treatment was significant (Table 3-2, Figure 3-5). However, the vertical trends were slightly different for the soil C: N ratio than either C or N concentration. In both locations, the highest C: N ratios (~30:1) tended to be found in the 10 - 20 cm increment, due to lower N concentrations rather than higher C concentrations in that soil layer. The lowest C: N ratio was found in the 20 - 50 cm layer and the degree of difference between the CW and CFW and the other two treatments (CC, CF) was greatest in this layer for both locations. Overall, the significant main effect of the CW treatments represented an increase of 11% for the C: N ratio relative to the CC treatments (Figure 3-5).

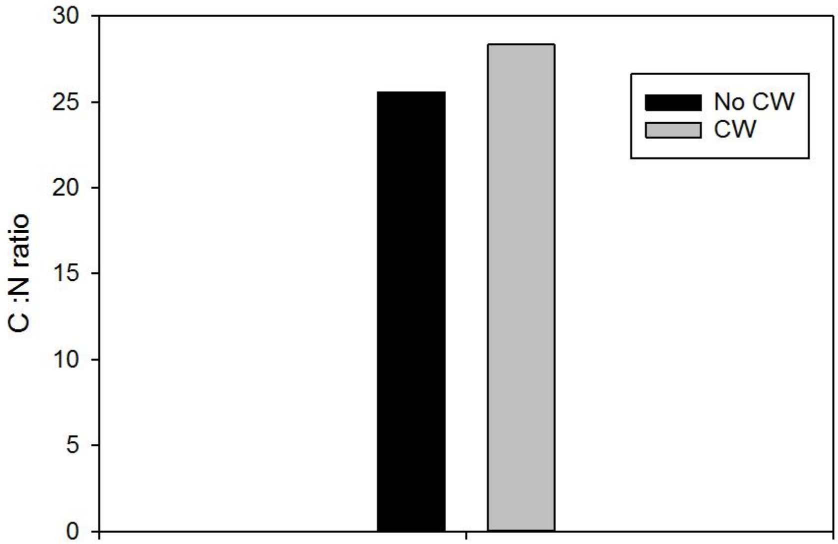

Figure 3-5. Significant CW main effect on soil C: N ratio for a 3-year-old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

III.4.5 Nitrogen and phosphorus extractions

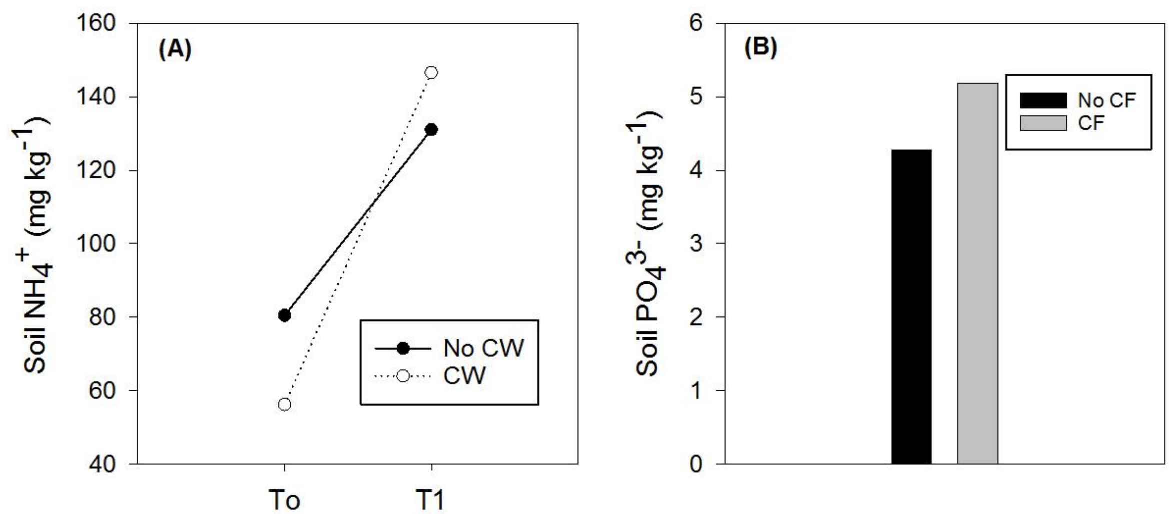

Figure 3-6. Significant (A) CW x T (T= incubation time) interaction effect on extractable ammonium and (B) CF main effect on soil extractable phosphorus for a three year- old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

The interaction effect of CW and T reflected a lower NH_4^+ concentration in the CW treatments at the beginning of the incubation (58 vs 81 mg kg^{-1}), but a greater rate of increase and similar concentration to the treatment receiving no prior W treatment that occurred by the end of the incubation (Figure 3-6A). The location and depth effects were more impactful than the treatments for NH_4^+. The NH_4^+ concentration significantly decreased from the 0 - 10 cm depth interval to the 20-50 cm depth interval for all treatments except for the CC treatment, a trend indicated by the significant main effect of depth (D). The main effect of location was significant and highlighted that, in general, the bed tended to have greater NH_4^+ concentrations than the interbed (Table 3-3). The significant effect of time indicated that the NH_4^+ concentrations were the greatest at the end of incubation across depth intervals and location, and this effect was more pronounced for the upper 0 - 10 cm depth interval. This trend also was supported by the L x D x T interaction effect (Table 3-3). Similar to NH_4^+ concentration, NO_3^- concentration significantly decreased with depth. The main effect of location was significant as well as the L x T interaction effect, suggesting greater NO_3^- concentration on the bed than the interbed positions at the end of incubation. In addition, the (D x T) interaction was significant and showed that NO_3^- concentrations were greater at the end of incubation than the initial concentration across depth intervals.

The PO_4^{3-} concentrations had similar trends as observed for NH_4^+ and NO_3^- concentrations. The D main effect was significant and showed the lowest concentration in the deeper soil. The CF main effect was significant (Figure 3-6B), and reflected a 21 % decrease in PO_4^{3-} concentration. The main effect of L, D and T and their interaction (L x D x T) were significant, highlighting greater PO_4^{3-} concentration than the interbed at the end of incubation across depth intervals.

Table 3-3. Statistical summary (ρ-values) of carry-over effect from first rotation fertilization (CF), weed control (CW), and their combination (CFW) on extractable ammonium, nitrate and phosphorus concentrations through time for soil depths (0 - 10 cm, 10 - 20 cm and 20 - 50 cm) of the bed and interbed locations of an untreated 3-year-old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

		$\mathbf{NH_4^+}$	$\mathbf{NO_3^-}$	$\mathbf{PO_4^{3-}}$
Effect	**DF**		***p*-value**	
CF	1	0.321	0.609	**0.002**
CW	1	0.630	0.068	0.082
L	1	**0.004**	**0.005**	**0.020**
D	2	**<.0001**	**<.0001**	**<.0001**
T (incubation time)	1	**<.0001**	**<.0001**	**<.0001**
CF x CW	1	0.242	0.630	0.146
CF x L	1	0.772	0.713	0.243
CW x L	1	0.429	0.754	0.413
CF x CW x L	1	0.922	0.256	0.511
CF x D	2	0.106	0.654	0.314
CW x D	2	0.573	0.054	0.577
CF x CW x D	2	0.375	0.584	0.844
L x D	2	0.124	0.167	**0.017**
CF x L x D	2	0.659	0.535	0.905
CW x L x D	2	0.901	0.985	0.734
CF x CW x L x D	2	0.550	0.790	0.729

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05)

Table 3-3. Continued

		NH_4^+	NO_3^-	PO_4^{3-}
Effect	**DF**		***p*-value**	
CF x T	1	0.804	0.675	0.545
CW x T	1	**0.030**	0.538	0.291
CF x CW x T	1	0.059	0.074	0.721
L x T	1	**0.024**	**0.009**	**0.006**
CF x L x T	1	0.362	0.898	0.785
CW x L X T	1	0.125	0.660	0.816
CF x CW x L x T	1	0.217	0.213	0.511
D x T	2	**<.0001**	**<.0001**	**<.0001**
CF x D x T	2	0.969	0.814	0.426
CW x D x T	2	0.627	0.607	0.278
CF x CW x D x T	2	0.532	0.415	0.795
L x D x T	2	**0.023**	0.125	**0.018**
CF x L x D x T	2	0.708	0.696	0.511
CW x L x D x T	2	0.618	0.931	0.556
CF x CW x L x D x T	2	0.837	0.802	0.773

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05)

III.5. Discussion

The productivity of pine plantations in the southeastern United States has increased 3-4 fold over the last several decades presumably because of genetic selection for improved growth and disease resistance, and improved silvicultural practices (Fox et al. 2007b, Jokela et al. 2010). What is effectively unknown is whether these increases in productivity can be expected to continue with repeated application of silvicultural techniques in the same plantation areas. Reductions in available nutrients, increases in pathogens, bedding techniques, or background changes in site conditions could combine to reduce site productivity in absolute terms, or could reduce a site's productivity potential relative to the regional potential. Comparisons of forest growth across rotations in the same location can be used to assess whether productivity has been diminished or increased in response to past treatments (Subedi et al. 2014). Here I found pine height growth in the first three years greatly exceeded growth in the previous rotation. For example, the second rotation's control plots were taller than in the most intensive treatments from the first rotation. This trend occurred at a site that was inherently very productive (Chapter II), but similar results have been observed in less productive sites (Subedi et al. 2014), suggesting an absolute decrease in early productivity should not be expected for these combinations of past- and current silvicultural treatments.

The productivity of pine plantations in the southeastern US is generally modified by nutrient availability, herbaceous and woody competition (Jokela et al. 2010), seedling quality (Allen et al. 1990, Neary et al. 1990, Jokela et al. 2010), soil moisture, and insects and diseases (Bengtson and Smart 1981, Belanger 1983). The greater growth in the second rotation was likely due to these limiting factors being altered by advances in silviculture and genetic selection, factors contrasted across rotations in Table 3-4. For example in the first rotation, the 23-33% mortality of trees at an early age (before 5 years) was likely due to nursery derived fusiform rust (*Cronartium fusiforme*

Hedg.) (Jokela et al. 2000) and 77% of trees were affected by tip moth (*Rhyacionia* spp.) (Tumushime unpublished), pests that were controlled in the second rotation, respectively, by genetic selection and nursery pesticides. Temperatures during the first and second rotations were similar, but precipitation was ~40% greater in the second rotation, which in this low-lying area would have been more likely to have negatively affected tree growth if not for the double bedding in the second rotation, as opposed to single bedding in the first rotation. Adding to the cultural advances across rotations, the ~47 µl l^{-1} increase in CO_2 could have increased annual productivity by 6-8% based on an interpolation of results from an elevated CO_2 experiment in a loblolly pine plantation (McCarthy et al. 2010). Some combination of these and the other factors in Table 3-4 contributed to the consistently positive absolute changes in growth across rotations, while the relative differences in productivity observed across the carry-over treatments may have been related to differences in nutrient supply.

Table 3-4. Potential contributing factors to a multi-rotational change in height growth for a 1-3-year-old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

Inter-rotational change	**First rotation (1988-1990)**	**Second rotation (2013-2015)**
Mean temperature[1]	21.2°C	21.3°C
Mean precipitation[1]	1089 mm	1455 mm
CO_2 concentration[2]	~352 µl l^{-1}	~399 µl l^{-1}
Seedling propagation	Bare-root	Containerized
Genetic Selection	1st Generation / open pollinated	2nd Generation / control pollinated
Bedding techniques	Single	Double
Tip Moth control	No	Yes
Herbicide for *Panicum*	No	Yes

[1]PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 9/9/17
[2] (Keeling et al. 2001)

The initial nutrient extractions suggested that nutrient availability was at least partially responsible for the variation in growth among the carry-over treatments. The second rotation tree growth was lowest in the CW, as was extractable NH_4^+ at the beginning of an incubation. Growth was greatest in the carryover CF plots, and this corresponded to greater extractable PO_4^{3-}, while the CFW growth was similar to the CC treatment. Subedi et al. (2014) also observed that early pine growth was greatest in the carry-over fertilizer treatment relative to the control and competition control treatments, and that growth differences correlated with greater exchangeable P, Mn and Zn across treatments. Comerford et al. (2002) reported that in Georgia U.S., enough residual fertilizer P was left in the soil after the harvest to satisfy the P demand of newly established pine plantation. Given the potential of nutrient carry-over effects to alter tree growth (Subedi et al. 2014), a key question is how long will past silvicultural practices affect nutrient dynamics and productivity after harvest.

Nutrient availability after a harvest reflects an interaction between the Assart effect, or the mineralization of nutrients derived from harvest detritus, and the inherent capacity of the soil to retain nutrients and supply them to the next rotation. Although fertilization in the previous rotation did increase P pools and extractions (Chapter II), a pattern consistent with the second rotation P extractions, eventually N demand by pine will increase with the development of the canopy (Dalla-Tea and Jokela 1994). Thus, the lack of change in the N pool could translate to reduced growth rate in the CF plots. The lower extractable NH_4^+ in the CW plots suggested that N was responsible for the lower growth but other nutrients may also limit growth in these systems, as observed for both macro- and micronutrients in fertilized pine plantations in the southeastern United States (Jokela et al. 1991, Huntington 2000, Kyle et al. 2005, Vogel and Jokela 2011, Carlson et al. 2014). Extractable concentrations for other macro- and micro- elements were not measured, but the reduced NH_4^+ for the initial extraction in the CW treatments could indicate lower availability of multiple nutrients (Subedi et al. 2014).

In the first rotation, fertilization alone with N and P had a non-significant effect on growth (Chapter II), but in this rotation there was a significant response to the RF treatment (Figure 3-2). This result also suggests that elements in addition to N and P may be growth limiting as the second rotation fertilization treatment included a suite of both macro- and micronutrients (Table 3-1), while in the first rotation only N, P and some Ca were added. First rotation growth indicated that this site had a relatively high inherent productivity (Chapter II), which suggests adequate nutrients were available for tree growth (Jokela and Martin 2000). However, recent research suggests inherent site productivity potential is not an indicator of whether other essential nutrients could be limiting to pine growth (Forest Biology Research Cooperative, personal communication) and multi-element combinations have produced greater growth than N and P in studies on similar soils (Albaugh et al. 2007, Roth et al. 2007). Moreover, Subedi et al. (2014) observed a much larger carry-over fertilization effect on a Spodosol that had received multiple applications of macro- and micronutrients. Thus, to accelerate pine growth, more diverse mixtures of macro- and micronutrient fertilizers may be warranted on these poorly drained Spodosols (Jokela et al. 1991, Albaugh et al. 2007, Vogel and Jokela 2011).

In the carry-over plots, both soil C and C: N ratio were increased by competition control, while soil N was greater. These trends followed those observed at the end of the first rotation (Chapter II). Polglase et al. (1992b) found a significant soil C:N and N increase associated with competition control treatment in a similar experiment early in rotation, but by the end of the rotation, this effect was no longer evident (Vogel et al. 2011). Similarly, Wood et al. (1992) found a decrease in substrate quality with understory removal in pine plantations. Although an increase in the soil C:N ratio suggests that the soil microbial community could immobilize N (Andariese and Vitousek 1988, Li et al. 2003), net N mineralization indexed by the laboratory incubation indicated that the previous rotation's competition control plots would eventually have relatively high mineralization. The dominance of pine litter relative to understory plants may have decreased bioavailable C (above and belowground labile C) (Gurlevik et al. 2004), reducing N immobilization potential and increasing mineralization in competition control plots. Ammonification was also significantly greater in the CW plots and made the largest contribution to net N mineralization in surface soils, suggesting the process of transforming organic matter to mineral N was still in its early stages in the incubation. Eventually, mineralization of N and other nutrients may counteract the negative effects observed for growth in the CW only plots (Figure 3-2).

The extractions of N and P often indicated immobilization potential for P or a shift from ammonification to nitrification in deeper soil depths. During the laboratory study, soil moisture content was kept near field capacity and temperature constant at 22-25 °C to maximize N and P mineralization (Kladivko and Keeney 1987, Goncalves and Carlyle 1994). In the case of P immobilization at 20-50 cm, the ideal laboratory conditions may have stimulated microbial growth and P immobilization because the in situ soils were near saturation at the time of collection. P immobilization occurred despite a long incubation period (1 year), which suggests that the microbial population or P precipitation was suppressed in situ.

The practice of double-passed bedding is generally done in areas with poor soil drainage so that seedlings can root above the water table, but the practice also reduces competition (reviewed in Morris and Lowery 1988). My research suggests the beds also have a positive influence on soil N and P availability early in rotation. Although a positive effect on nutrient availability was previously described for site preparation (Vitousek and Matson 1984, Morris and Lowery 1988), soil bedding effects on depthwise change in nutrient availability has not been previously reported. The results here suggest that bedding may increase nutrient availability generally and also with depth, especially for P. With increased extreme precipitation events possible for the southeastern United States over the next century (Wuebbles et al. 2014), bedding could be a critical practice needed to maintain pine productivity.

III.6. Conclusions

The results from this study suggests inter-rotational increases in pine productivity are, overall, much greater than carry-over effects. Still, the carry-over effects do suggest some modification of silviculture in the second rotation that takes into account past treatments could further improve forest growth and the efficiency of fertilizer use. For example, the negative carryover effect of competition control on tree size may have been related to available N, requiring early N fertilization. A slight positive carryover effect of past fertilization may have been due to increased P availability, requiring lower second rotation P fertilization. Overall, the application of a more complete fertilizer mix and competition control in the second rotation greatly enhanced productivity and could be indicative of how modern silviculture applications could further improve growth in these pine plantations.

CHAPTER IV

SLASH PINE AND LOBLOLLY PINE DIFFER IN NUTRIENT DYNAMICS UNDER COMPETITION CONTROL AND FERTILIZATION, BUT SILVICULTURE HAS GREATER CARRY-OVER EFFECTS

IV.1. Synopsis

The nutrient cycling response of loblolly pine *(Pinus taeda* L.) and slash pine (*Pinus ellioti var.elliotti* Engelm) to silvicultural treatments was contrasted for a plantation both at the end of the past rotation and at the beginning of the next rotation. At age 26 years, the P pools in tree biomass, surface organic horizons, and soils were estimated, and after harvest, carry-over effects from the first- to the early second-rotation were evaluated at the time of planting for soil C, N, and P concentrations, and N and P availability. The experimental design was a split-plot with species (S) as the split and fertilization (F), competition or weed control (W), and the combined application (FW) as treatments. At the end of the rotation, slash pine tended to have lower P concentrations than loblolly pine in foliage and root tissues, with significantly lower values for bark ($p=0.005$). The P concentrations of species' tissues interacted differently with silviculture, with significant S×W interactions for P in roots >2 mm reflecting larger reductions in P concentrations in slash than loblolly pine roots under the W treatments. For roots <2 mm, an S×F×W interaction occurred because P concentrations in loblolly pine roots increased in response to both F and W, but slash pine only increased in response to F. Slash pine also had significantly lower P content in the Oe+Oa layer. In the 33-66 cm soil layer, slash pine retained more soil P than loblolly pine in the W treatment. The F treatment increased P for both species' foliage, the Oi and Oe+Oa layers, and the soil in the 33-66 cm layer. At the beginning of the next rotation, the species effect was not evident in

soil nutrients but species did have a significant effect on extractable N and P, where loblolly pine had greater extractable NH_4^+ and PO_4^{3-} than slash pine. In contrast to species effects, fertilization consistently increased the next rotation soil C, N and P. Also, past fertilization increased extractable NO_3^- and interacted with completion control to increase extractable NH_4^+ and PO_4^{3-}. These results suggest that species effects may be significant, but silvicultural treatments will have a greater effect on site productivity potential.

IV.2. Introduction

The pine plantations of the southeastern United States are managed for commercial purposes and, as such, management decisions are generally focused on maximizing profitability (Smith et al. 1994). One important decision that greatly affects profitability is what species to plant and what types of silvicultural treatments to apply (Jokela 2004). The two most commonly planted pine species in the region, loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) (Fox et al. 2007b), differ in response to silvicultural treatments (Jokela et al. 2010). Loblolly pine often grows faster than slash pine during early rotation and responds more favorably to silvicultural treatments involving fertilizer (Jokela and Martin 2000, Shiver et al. 2000). However, slash pine nutrient use efficiency is greater than loblolly pine (Colbert et al. 1990, Dicus and Dean 2008), and during periods of high fertilizer and low commodity prices, unfertilized slash pine plantations may provide higher financial returns than fertilized plantations (Stearns-Smith et al. 1992).

Since the early 21st century, there has been a trend for more wider natural range loblolly pine being planted than slash pine in the southeastern United States (South and Harper 2016), and overall, pine plantations are expected to continue to increase in extent by the year 2040 across the region (Wear and Greis 2002a). These trends suggest that many plantations that were once slash pine may become loblolly pine plantations in the future. This transformation of the region's plantations toward dominance by one species could affect ecosystem C and nutrient cycling, because of how these species interact with silvicultural treatments. For example, in a comparison of the two species' C accumulation, a slash pine stand receiving only competition control stored more C in tree biomass at the end of rotation than did loblolly pine stands receiving competition control, fertilization, and fertilization plus competition control (Vogel et al. 2011). Some studies have reported that an increase in fertilization intensity negatively affects slash pine biomass relative to loblolly pine biomass at the same site, often because of greater pitch canker (*Fusarium circinatum* Nirenberg & O'Donnell) infection in slash pine (Roth et al. 2007, Zhai et al. 2015). The mineralization of P from litter has also responded differently to silvicultural treatments for the two species (Polglase et al. 1992c), and relative amounts of fertilizer N retention have differed in response to whether competition control and fertilization were separate or combined for the two species (Vogel et al. 2011).

There has been increasing scientific and forest industry interest in the carry-over effects and sustainability of silvicultural practices across multiple rotations (Subedi et al. 2014). Studies have generally focused on the effect of fertilizer or competition control on a single species' growth in the next rotation (Comerford et al. 2002), often in the context of the effect of fertilization on nutrient pools (Gentle et al. 1986, Everett and Palm-Leis 2009, Kiser and Fox 2012). Loblolly pine litter generally has higher nutrient (N and P) concentrations than slash pine (Polglase et al. 1992b, Dicus and Dean 2008), possibly leading to higher N and P mineralization in stands of loblolly pine than in slash pine. Previous work documented that greater stand volume in loblolly pine than slash pine plantations was positively correlated with N mineralization (Dicus and Dean 2008). In addition, Polglase et al. (1992) found greater P release from the decomposing litter of loblolly pine than slash pine, possibly explaining its greater productivity, and highlighting the potential species effect on long-term site productivity.

The purpose of this study was to contrast nutrient dynamics in slash pine and loblolly pine as these species respond to silvicultural treatments both at the end of a 26-year rotation, and at the beginning of the next rotation. Estimates of ecosystem pools of P, along with a previous study of C and N pools (Vogel et al. 2011), were used at the end of rotation to estimate how species selection (slash pine vs loblolly pine) interacted with the cumulative effects of fertilization, competition control, and their combined application at the Intensive Management Practices Assessment Center (IMPAC) site located near Gainesville, Florida, USA. At the beginning of the next rotation, soil C, N, and P concentrations and laboratory assessments of N and P availability were used to estimate how patterns observed at the end of rotation carried over into early rotation soil nutrient dynamics and these results compared to the early growth reported by Subedi et al. (2014). The primary hypothesis tested was that relative to slash pine, loblolly pine's greater nutrient demands would support greater P pools at the end of rotation, and that N and P cycling would be greater in loblolly pine stands at the beginning of the following rotation.

IV.3. Materials and methods

IV.3.1 Study site description

In 1983, the original IMPAC experiment was established by the University of Florida and United States Forest Services to evaluate the effects of intensive management practices on southern pine forest productivity (Jokela et al. 2010). Located near Gainesville, Florida (29°30′N, 82°20′W), the study site has a mean annual temperature of 20.5°C (1981-2011) and an approximate mean annual precipitation of 1178 mm (NOAA, 2012). At the end of a 26-year rotation, a C and

N budget was estimated for above- and belowground components at the IMPAC site (Vogel et al. 2011). From these samples, the P accumulation was estimated for aboveground vegetation, surface organic horizons, roots, and soil. In 2009, the IMPAC site was continued as a carry-over and continuous silvicultural treatment experiment called IMPAC II. This new study has been focused on estimating carryover and continuous treatment effects on planted loblolly pine (Subedi et al. 2014). Within 3 weeks of planting of IMPAC II in December 2009, but before fertilization treatments were applied, soil was collected to estimate the carry-over effects on soil C and N pools, and N and P availability.

The soils of the site are dominated by poorly drained Ponoma fine sands (sandy, siliceous, hyperthermic Ultic Alaquods) (Polglase et al. 1992b). Surface particle size analysis (Bouyoucos 1962) for the soils at this site indicated averages of 89% sand, 4.8% silt and 6.2% clay and the soil had pH 4-5 (Table 4-1). A common profile at the site had the spodic horizon between 20 - 50 cm, and an argillic horizon at 90 - 120 cm, with the depth to these diagnostic horizons varying among blocks within the site (Vogel, personal observation). The soil's low nutrient capital is related to the low organic matter content and cation exchange capacity (<5 $cmolc \cdot kg^{-1}$) (Jokela and Martin 2000), and the mixture of quartz sand and the few primary and secondary minerals (Polglase et al. 1992b).

Table 4-1. Average (± SE) soil pH and particle size distributions (g kg^{-1}) 1-year following a harvest of a 26-year-old loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii var.eliottii*) stands near Gainesville, FL.

Soil depth (cm)	Treatment	pH	Sand	Silt	Clay
	Loblolly pine				
0-20	C	4.5 (0.2)	887 (4)	47 (12)	65 (8)
	F	4.3 (0.1)	859 (11)	73 (10)	68 (2)
	W	4.5 (0.1)	890 (8)	47 (9)	63 (1)
	FW	4.2 (0.1)	895 (3)	41 (3)	64 (1)
20-40	C	4.8 (0.2)	916 (5)	29 (11)	55 (6)
	F	4.4 (0.2)	884 (28)	55 (34)	62 (7)
	W	4.4 (0.2)	880 (19)	53 (29)	67 (10)
	FW	4.3 (0.2)	903 (1)	39 (6)	58 (7)
	Slash pine				
0-20	C	4.3 (0.1)	891 (4)	50 (6)	59 (2)
	F	4.4 (0.1)	895 (1)	63 (3)	63 (2)
	W	4.2 (0.1)	897 (5)	44 (15)	58 (10)
	FW	4.0 (0.1)	874 (1)	61 (9)	64 (8)
20-40	C	4.5 (0.2)	893 (14)	40 (3)	67 (11)
	F	4.6 (0.3)	903 (5)	39 (11)	58 (6)
	W	4.5 (0.2)	894 (4)	40 (7)	67 (10)
	FW	4.0 (0.1)	875 (3)	63 (13)	62 (11)

IV.3.2 Study Designs and Treatments

The IMPAC experiment (Figure 4-1) consisted of a split-plot design with slash pine and loblolly pine as the split, and identical treatments having controls (C), fertilization (F), competition or weed control (W), and the combined application of treatments (FW). The treatments were randomized within three blocks. Trees were hand planted at a 1.8 m x 3.0 m spacing (Martin and Jokela 2004), with the whole plot equivalent to 820 m^2 and with an interior measurement plot consisting of five beds and eight trees per bed for a total 40 trees per plot (equivalent area 260 m^2).

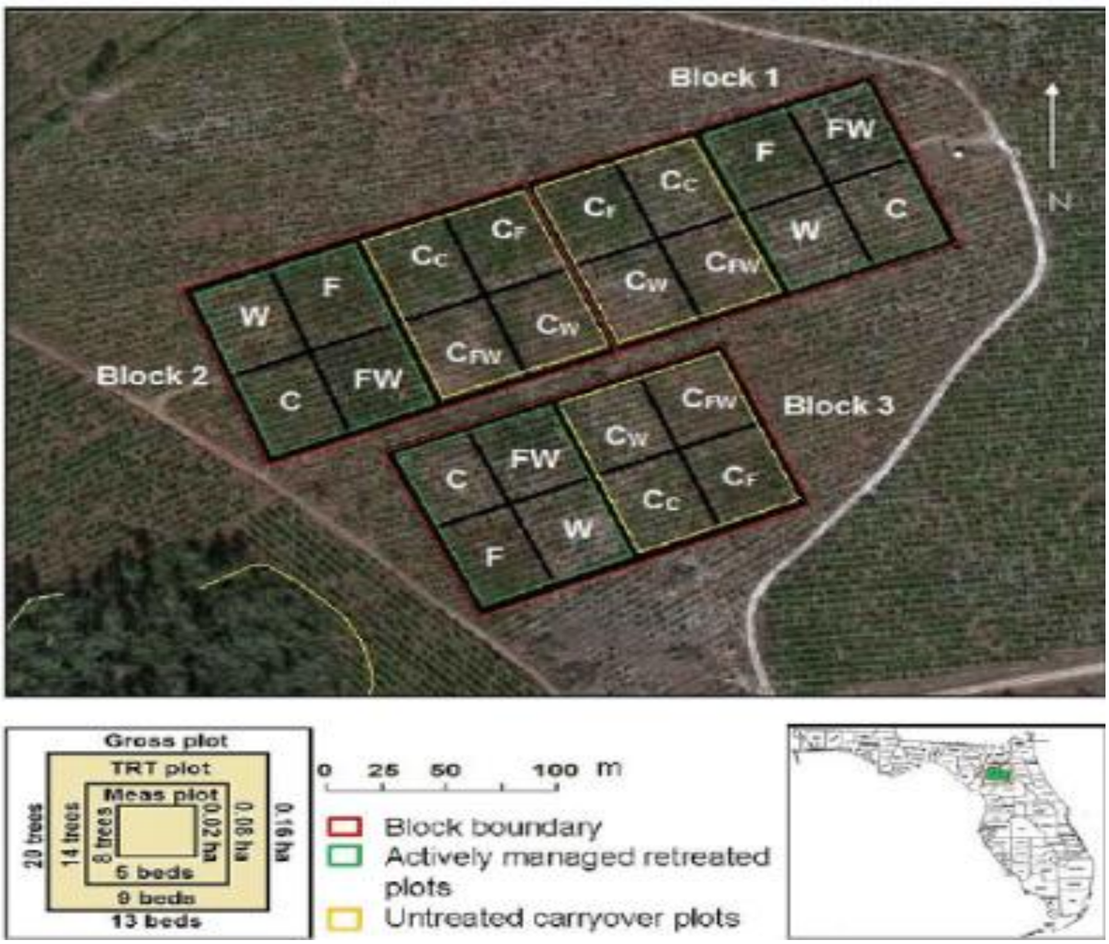

Figure 4-1. IMPAC experimental design and treatments

Along the beds, an untreated six-tree buffer (~12 m) separated treatment plots, and across the beds, the spatial equivalent of four untreated beds (~12 m) separated adjacent plots.

Prior to IMPAC's establishment, the overstory vegetation was a slash pine plantation. After harvest, the residual material was moved from the plots to a central landing area. The experimental site was then mechanically prepared using a single-pass bedding treatment (Neary et al. 1990). In 1983, first-generation genetically improved (1-0) bare root seedlings of open-pollinated loblolly pine and slash pine sources were hand planted (Martin and Jokela 2004). For the fertilization treatments, the combination of several different macro- and micronutrient fertilizers were annually applied at different rates from ages 0-10 and 16-18 years (Table 4-2). The fertilizer treatments were applied in semicircular bands about 0.5 m from the base of each tree. For the first 10 years, the understory vegetation competition was controlled annually using different herbicides applied at labeled rates and stopped after canopy closure due to the suppression of competing plants vs the overstory in the competition control treatment plots (W and FW).

Table 4-2. IMPAC fertilizer application rates and timing for the loblolly pine (Pinus taeda) and slash pine (Pinus elliottii var. elliottii) experimental sites receiving either fertilizer only or fertilizer plus weed control.

		Mean annual application rate (kg ha^{-1} year^{-1})										
Time period	Stand age	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn	B	S
1983-1993	0-10	36.0	14.3	31.7	10.8	7.2	0.3	0.3	0.05	0.3	0.05	7.2
1998-2000	15-17	242.2	29.0	37.7	0	0	0.4	0.8	0.13	0.3	0.13	0

Preparation for the IMPAC II experiment began before the harvest of IMPAC I. In April 2009, the understory vegetation in C and F plots was mulched to maintain its nutrient capital onsite. Because the understory vegetation had been suppressed by herbicide application in the W and FW plots, mulching was not necessary in these plots. The overstory trees were harvested in May 2009 at age 26 years using whole- tree harvesting and tree brunt a central landing. This approach was meant to avoid disturbing the forest floor but it also meant that nutrient capital in branches and foliage were removed from the treatments. After harvest, the site received a single-pass bedding in June, and then a second bedding pass late in August of 2009. Containerized 2nd generation seedlings that were a known cross of high-performing loblolly pine families were hand-planted in December 2009. To maintain a weed-free environment, only the actively retreated plots (W and FW) received follow-up herbicide applications in October 2009 (broadcast application of 1035 l ha^{-1} of Imazapyr (0.9kg), 340 ml ha^{-1} of Garlon 4 and 150 ml ha^{-1} Escort). This application occurred prior to the soil collection but was expected to have little effect on nutrient cycling. Fertilizer was not applied before soil collection.

IV.3.3 Measurements

End-of-rotation measurements of tree height and diameter at breast height (DBH) at the IMPAC site were made in December 2009, one year before the final harvest (Vogel et al. 2011). Prior to the 25th year, the same measurements were conducted every 1-2 years (Jokela et al. 2010). To estimate the aboveground biomass estimates for loblolly pines and slash pine at the age 25 years were made using a combination of specific-site and allometric equations described in Vogel et al. (2011). Briefly, the allometric equations developed by Jokela and Martin (2000) were used to predict the foliage, branch, stem wood and stem bark biomass. For the trees larger than the diameter used in Jokela and Martin (2000) equations, the Naidu et al. (1998) and Jokela et al. (2009) equations were used for loblolly and slash pines, respectively.

IV.3.4 Sampling and analysis

For the original IMPAC site, a detailed description of aboveground tissue collection was provided in Vogel et al. (2011). Briefly, aboveground tissues were collected in 2001 and 2009 at stand age 18 and 26 years, respectively. The sampling consisted of randomly selecting in each plot three dominant or co-dominant trees. Foliage and branches were then randomly collected from felled trees per treatment plot. Because some trees were removed from the plots before stem wood could be sampled, stem wood tissue P concentrations for the 18-year old stand were used for age 26 years to complete the nutrient budget. P content was then estimated by multiplying the dry mass by the corresponding P concentrations.

Forest floor was collected for P concentration analysis. Six forest floor samples were collected in each plot from a 20.3 cm diameter ring. Three samples were randomly collected on bed and interbed locations and then separated into Oi and Oa + Oe horizons. Each forest floor horizon was thoroughly mixed within a bed and inter-bed position and a composite sample was created. For the Oe+Oa horizon, the sample was sieved to separate three components that are forest floor, organic matter, and mineral soil. The Oe+Oa layer contained a large amount of mineral soil and this amount was analyzed separately and added back to the Oe+Oa layer. The forest floor samples (Oi and Oe + Oa) were then ground with a Wiley Mill to pass a 20-mesh screen. Soil samples were collected at the same location where the forest floor was collected within each plot using a 7.62 cm diameter auger, one year prior to the forest harvest at age 25 years. In all sampling positions, mineral soil samples were collected at depth intervals of 0 - 33 cm, 33 - 66 cm, and 66 - 100 cm at the original IMPAC site.

For the IMPAC II experiment, the 0 - 20 cm and 20 - 40 cm soil depths were randomly sampled from the bed and interbed position in the fall of 2009. Because the soil was saturated, the sampling was stopped at a 40 cm depth as a deeper soil could not be retrieved. Three samples were collected in each treatment plot and for the bed or interbed position (6 total). The samples were thoroughly mixed by plot, treatment, depth and position to make composite samples. About 1000 g was subsampled and then used for nutrient analysis. These samples were weighed wet and stored at 4 ˚C until processed.

Prior to analysis, soil samples were passed through a 2 mm sieve. Roots and large wood fragments were removed, rinsed with distilled water, dried at 65 °C, and weighed. Subsamples (~100 g) of the passed-through mineral soil were oven-dried at 105˚C for bulk density determination, and dried at 65˚C for pH and nutrient content measurements. These latter soils were ground on a roller ball mill for at least 48 hours or until fully pulverized. Soil pH was estimated using an Accumet Basic pH meter (Denver Instrument, Arvada, CO, USA) and a 1:2 soil to water ratio. Soil organic C and total N were determined by dry combustion using an elemental analyzer (Thermo Finnigan FLASH EA 1112). To determine soil P, about 0.5 g of the ground and re-dried sample was dry-ashed in a muffle furnace at 450°C for four hours and mixed with aqua regia (1:3 HNO_3: HCl) extracting solution. The extract passed through Q5 filter papers pre-rinsed with 1% nitric acid and then was analyzed using inductively coupled plasma atomic emission spectroscopy (ICP-AES; Chemistry Laboratory, Texas A&M University, TX, USA). The 1,000 ppm phosphorus AA standard (Ammonium dihydrogen phosphate in water) was used to assess the accuracy of the P measurements. For the aboveground tissues, forest floor and roots, P along with macro- (K, Ca, Mg, and S) and micro-nutrients (B, Cu, Fe, Al, Mn, Mo, Na, and Zn) were analyzed using inductively coupled argon plasma unit (ICAP; Micro-Macro International Laboratory, Athens, GA). Certified standards were used to assess the accuracy of the above nutrient's measurements.

The IMPAC II soil N and P availability were evaluated using a benchtop incubation conducted at room temperature (20-25°C) for 120 days to estimate the effect of treatments on N and P mineralization for the carryover and retreated plots. Extractable N and P analyses were performed on the incubated soils using potassium chloride (KCl) and Mehlich III extraction methods on four soil subsamples pulled from the jar at 30-day intervals. To prepare the KCl extract, 3.0 g of soil was mixed with 30 ml of 1.0 M KCl extracting solution (soil: solution ratio 1:10) and placed on a shaker for 30 minutes (120 oscillation/minute). To prepare Mehlich III extract, about 3.0 g of soil was mixed with Mehlich III extracting solution (soil: solution ratio 1:10) and placed on a shaker for 5 minutes (120 oscillations/minute). Extracts were filtered through pre-rinsed Q2 filter papers into scintillation vials and frozen until analysis. KCl extraction was used to extract for NO_3^--N and NH_4^+-N (Keeney and Nelson 1982) and a Mehlich III extraction was used to extract for available P (PO_4^{3-}) (Mehlich 1984). Different chemical reactants were added to the samples that changed the colors of solutions. Salicylate and bleach solutions, Vanadium cocktail solution and Malachite Green solution were added to $NH4^+$, NO_3^- PO_4^{3-} samples, respectively. Solution color was blue green for NH_4^+, pale to bright pink for NO_3^- and green for PO_4^{3-} and were read at read at different wavelengths: 650 nm, 540 nm and 630 nm, respectively using the colorimetric method with a spectrophotometer EON Microplate reader (Biotek Instruments, Inc.). Prior to measurements, Ammonium standard, Nitrate standard and 1,000 ppm phosphorus AA standard were used to assess the accuracy for $NH4^+$, NO_3^- and green for PO_4^{3-}, respectively. For the incubation, soil moisture was brought to near field capacity and incubated on the benchtop at room temperatures (~22°C-25°C). Net N and P extractions were made monthly.

The soil texture was analyzed using the Bouyoucos hydrometer method (Bouyoucos 1962). Briefly, 50 g of oven-dried at 65 °C soil that passed through a 2-mm sieve was mixed with a dispersing agent (2.5 N sodium hexametaphosphate, $(NaPO_30)_6$) and deionized water. A calibrated hydrometer was inserted into the suspended materials for 40 seconds and the hydrometer reading gives the amount of suspended silt and clay particles per liter while the sand particles are settled at the bottom of the cylinder. After 2 hours settling, another hydrometer reading was recorded that gives the amount of suspended clay particles per litter. The sand fraction was calculated based on the amount of clay and silt in a sample. The hydrometer readings were corrected according to the temperatures measured at both readings. The texture class was determined using the soil textural triangle proposed by USDA. The soil samples were not subject to the organic matter and carbonates removal considering the excessively weathered soils and low pH of 4-5.

IV.3.5 Statistical analysis

Statistical analyses were performed with the SAS PROC mixed model procedure (Littell et al. 1998) (SAS Institute Inc., 1988) using a split plot analysis of variance (ANOVA). The effects of species and silvicultural treatments were determined for P concentrations and contents in vegetation tissues, forest floor, roots, and soil for IMPAC I. Analysis for IMPAC II was only investigated for soil C, N, and P concentrations, and N and P availability. Species and the treatments (F, W) were treated as fixed effects while blocks and block x species in the split plot were treated as random effects. Block was not significant for any variable and was not included in the output. Turkey's studentized range (HSD) test was used for treatment means separation with an alpha level of 0.05. The P concentrations for stem and branch wood were only collected for loblolly pine at age 18 and, therefore, the analyses only focus on P contents.

IV.4. Results

IV.4.1. Intensive Management Practices Assessment Center I (IMPAC I)

IV.4.1.1 Phosphorus concentration and pools

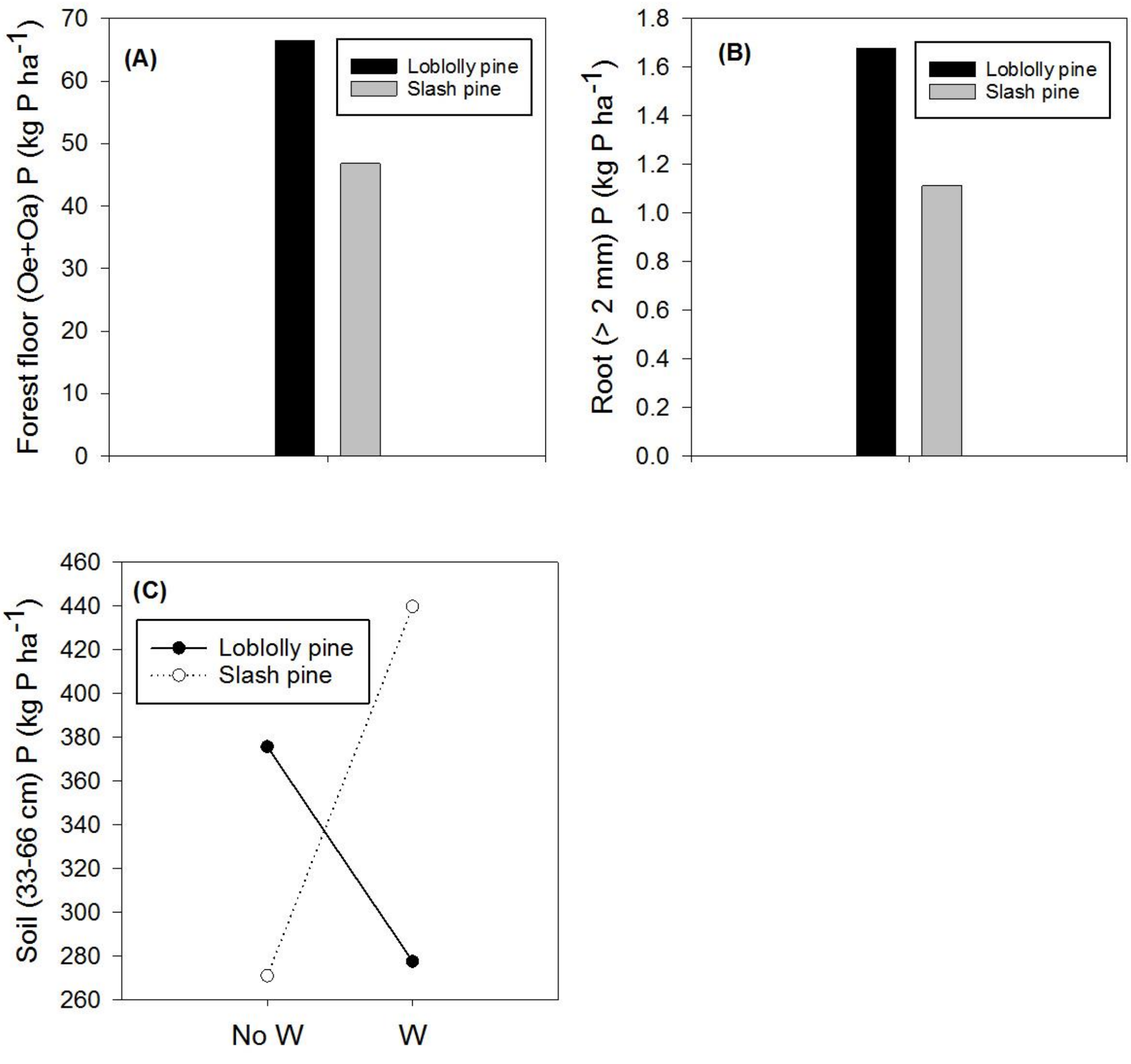

Figure 4-2. Significant main effect of species for (A) forest floor Oe+Oa layers and (B) root (> 2 mm) and (C) W x S (species) interaction effect for soil (33 - 66 cm) on P content for a 26-year-old loblolly pine and slash pine plantation near Gainesville.

Foliage had the highest P concentration of all vegetation pools, ranging from 0.84 - 0.91 g kg^{-1} in the loblolly pine foliage, and 0.76 - 0.92 g kg^{-1} in the slash pine foliage (Table C-1). The second highest P concentrations were found in the root pools, which ranged from 0.36 - 0.65 g kg^{-1} in the < 2mm roots, and from 0.20 - 0.72 g kg^{-1} in the >2 mm roots. The <2 mm root P concentrations had a significant S x F x W interaction (Table 4-3), which highlighted a proportionately greater increase in root P concentration for loblolly pine than slash pine for both the F and W treatments (Table C-1). For roots >2 mm, a significant S x W interaction (Table 4-3) corresponded to a decrease in the P concentration with the competition control treatment for both species, but the decrease was proportionately greater for slash pine (62%) than for loblolly pine (35%) (Table C-1). The S main effect was significant (p=0.005) for bark (Table 4-3), indicating greater P concentration in loblolly pine than slash pine bark. Species differences for P concentrations also occurred for the Oe+Oa detrital layer as a main effect, and in the 33 - 66 cm soil layer as an S x W interaction (Table 4-3). These concentration differences translated to P pool differences that were larger than for vegetation (Figure 4-2A-C, Table C-2), as the soil and organic layer pools of P were much larger than vegetation pools (Table C-2). Significant species differences for some pools (detrital wood, roots > 2mm) reflected much less change in mass than that of the Oe+Oa layer. Detrital wood of slash pine stored 0.6 kg ha^{-1} more P than did loblolly pine (Table C-2), while the forest floor of loblolly pine stored 20 kg ha^{-1} more P than slash pine (Figure 4-2A) and roots >2 mm, 0.4 kg ha^{-1} (Figure 4-2B). The S x W interaction for the 33 - 66 cm soil layer indicated a much greater (162 kg ha^{-1}) pool of P under slash pine than for loblolly pine under the W treatment (Figure 4-2C).

Table 4-3. Statistical summary of p-values for main and interaction effects of species and treatments on P concentration (g kg^{-1}) in aboveground vegetation, forest floor, roots, and soil for a 26-year-old loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii* var.*elliottii*) stands near Gainesville, FL treated with fertilization (F), competition control (W), and fertilization combined with competition control (FW). Branch and stem wood were only measured for loblolly pine.

	Aboveground components				Forest floor		Roots (mm)		Soil depth interval (cm)			
Effect	Foliage	Bark	Branch[1]	Stem[1]	Wood	Oi	Oe+Oa	<2	>2	0-33	33-66	66-100
F	**0.004**	0.841	0.590	0.100	**0.046**	**<0.001**	**0.045**	0.010	0.125	**0.038**	**0.033**	0.401
W	0.650	0.324	0.590	0.100	0.477	0.177	0.383	0.640	**<0.001**	0.602	0.447	0.445
F x W	0.860	0.199	0.120	0.100	0.903	0.280	0.073	0.012	0.365	0.991	0.141	0.979
S	0.200	**0.005**	--	--	0.260	0.282	**<0.001**	**0.001**	0.229	0.175	0.708	0.950

[1]Analysis is for loblolly pine only.

DF =1 for all main and interaction effects

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table 4-3. Continued

	Aboveground components				Forest floor			Roots (mm)		Soil depth interval (cm)		
Effect	Foliage	Bark	Branch[1]	Stem[1]	Wood	Oi	Oe+Oa	<2	>2	0-33	33-66	66-100
S x F	0.271	0.498	--	--	0.365	0.709	0.314	0.847	0.966	0.093	0.871	0.324
S x W	0.417	0.199	--	--	0.969	0.813	0.089	0.649	**0.032**	0.308	**0.011**	0.173
S x F x W	0.588	0.779	--	--	0.231	0.605	0.573	**0.017**	0.924	0.900	0.267	0.716

[1]Analysis is for loblolly pine only.

DF =1 for all main and interaction effects

Effects with bold numbers are significantly different effects (Tukey’s HSD at alpha=0.05).

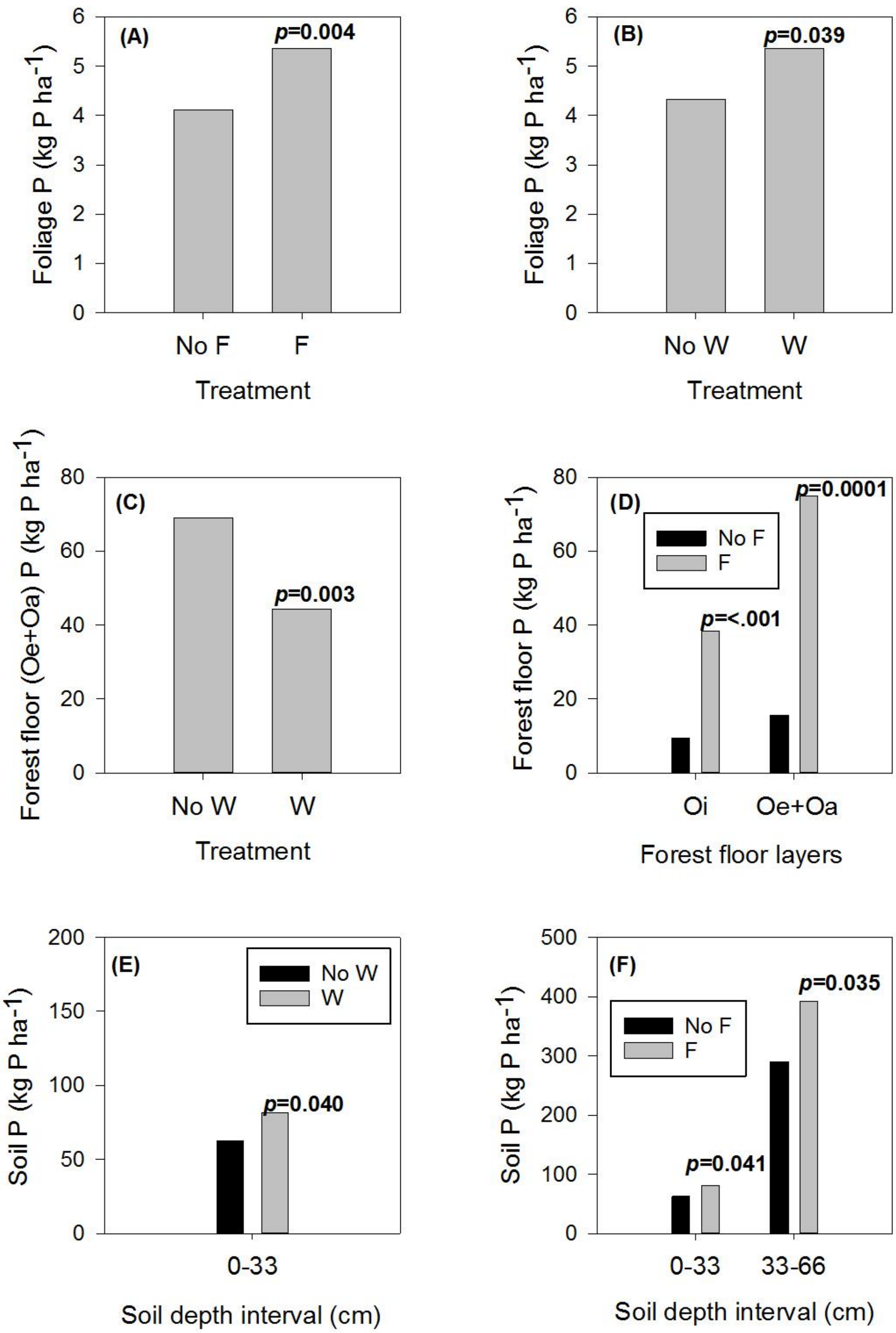

Figure 4-3. Significant F main effect for (A) foliage, (D) forest floor Oi and Oe+Oa layers and (F) soil (0 - 33 cm and 66 - 100 cm) and W main effect for (B) foliage, (C) for forest floor Oe+Oa) and (E) soil (0 - 33 cm) on P content for a 26-year-old loblolly pine and slash pine plantation near Gainesville.

Silviculture main effects were found for multiple P pools, with some effects reflecting change in both concentration and mass and others only mass. Fertilization significantly increased foliar P content (p=0.004) (Figure 4-3A) as did the W treatment (Figure 4-3B) because of changes in both concentration (Table C-1) and biomass. For the roots, the W main effect was significant and represented a decrease of P concentration and mass in roots > 2mm (p <0.0001) for both species (Table 4-4). A significant S x F interaction for stem mass (Table 4-4) was the result of greater biomass in the fertilized loblolly pine plots because the P concentration value was the same between species.

The W main effect for the Oe+Oa layer was significant (Figure 4-3C), but F x W interaction effect was not significant (Table 4-4). P content of Oi layer was the highest when fertilizer was applied with competition control for both species (Table C-2). The Oi layer ranged from 9.3 - 15.2 kg P ha^{-1} and the Oe+Oa from 42.9 - 108.3 kg P ha^{-} (Table C-2), with a significant F main effect reflecting increases for both forest floor layers (Figure 4-3D).

For the soil, he W main effect for 0 - 33 cm (p=0.040) depth interval was significant and represented an increase in P relative to the control treatment (Figure 4-3E). The F main effect was significant for the 0 - 33 cm (p =0.041) and the 33 - 66 cm (p =0.035) depth intervals and represented an overall increase in soil P (Figure 4-3D). The significant interaction effect of S x W for the 33 - 66 cm depth interval (p=0.007) represented a decrease of soil P for loblolly pine but an increase for slash pine (Table C-2). For the 66 - 100 cm depth interval, there were neither a significant main effect nor interaction effects of treatments, reflecting no differential response of two the species to treatments in the deeper soil horizons. There was no significant interaction effect of the S x F x W for any P pools (Table 4-4).

Table 4-4. Statistical summary of p-values for main and interaction effects of species and treatments on P content (kg P ha^{-1}) in above-ground vegetation, forest floor, roots, and soil for a 26-year-old loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii* var.*eliottii*) stands near Gainesville, FL treated with fertilization (F), competition control (W), and fertilization combined with competition control (FW).

	Aboveground components				Forest floor		Roots (mm)		Soil depth interval (cm)		
Effect	Foliage	Bark	Branch	Stem	Wood	Oi	Oe+Oa	<2	>2	0-33	33-66	66-100
F	**0.004**	0.120	0.315	**0.004**	0.096	**<0.001**	**0.0001**	0.611	0.227	**0.041**	**0.035**	0.262
W	**0.039**	0.063	0.520	**0.001**	0.881	0.103	**0.003**	**<0.001**	**<.0001**	**0.040**	0.435	0.402
F x W	0.250	0.276	0.255	0.678	0.703	0.097	0.146	0.195	0.405	0.688	0.168	0.949
S	0.169	0.239	0.691	0.593	**0.020**	0.067	**0.013**	**0.014**	0.997	0.188	0.523	0.981

DF =1 for all main and interaction effects

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table 4-4. Continued

	Aboveground components				Forest floor			Roots (mm)		Soil depth interval (cm)		
Effect	Foliage	Bark	Branch	Stem	Wood	Oi	Oe+Oa	<2	>2	0-33	33-66	66-100
S x F	0.714	0.101	0.312	**0.037**	0.234	0.117	0.110	0.704	0.804	0.091	0.714	0.313
S x W	0.661	0.790	0.284	0.629	0.492	0.728	0.839	0.278	0.465	0.255	**0.007**	0.173
S x F x W	0.614	0.876	0.307	0.435	0.147	0.651	0.833	0.993	0.641	0.894	0.260	0.829

DF =1 for all main and interaction effects

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

IV.4.2 Second Rotation-Soil Chemical and Physical Characteristics

Soil pH across the study site was acidic. For the past loblolly pine plots, it ranged from 4.0 - 4.4 and 4.0 - 4.6 in the 0 - 20 cm and 20 - 40 cm depth intervals, respectively and from 4.2 - 4.3 and 4.3 - 4.4 in the corresponding slash pine plots and depths. Soil texture analyses showed that the site was sandy across the entire study area and throughout the soil profile. Sand concentration was higher in the deeper soils than the surface soils for all treatments of the slash pine, ranging from 874 - 897 g kg^{-1} in the 0 - 20 cm depth, and 875 - 903 g kg^{-1} in the 20 - 40 cm depth. In the loblolly pine plots, sand concentrations ranged from 859 - 895 g kg^{-1} in 0 - 20 cm depth interval, and 884 - 903 g kg^{-1} in the 20 - 40 cm depth interval. Different trends were observed for silt and clay concentrations across treatments and depth intervals. Silt concentrations ranged from 44 - 63 g kg^{-1} in the 0 - 20 cm depth interval and 39 - 63 g kg^{-1} in the 20 - 40 cm depth interval of slash pine plots, 41 - 73 g kg^{-1} in the 0 - 20 cm depth interval and 39 - 55 g kg^{-1} of loblolly pine plots. Clay concentrations ranged from 58 - 64 g kg^{-1} in the 0 -20 cm sampling depth and 58 - 67 g kg^{-1} in the 20 - 40 cm sampling depth of the slash pine plots, and 63 - 68 g kg^{-1} in the 0 - 20 cm sampling depth and 58 - 67 g kg^{-1} in the 20 - 40 cm sampling depth of the loblolly pine plots. Neither soil pH nor soil particle size was affected by treatments ($p > 0.05$).

IV.4.3 Soil total carbon

Soil total C decreased with soil depth interval for both previous slash pine and loblolly pine plots. The decrease in soil C concentration with depth interval was only significant ($p < 0.05$) and noticed in the CF and CFW treatments for the highest depth. Soil C was 50% and 123% greater in the 0 - 20 cm depth interval than in the 20 - 40 cm depth interval for the CF and CFW treatments, respectively (Table C-4). For both species, CF significantly increased soil C in the 20 - 40 cm depth interval (Figure 4-4), while CFW had the highest C in the 0 - 20 cm depth interval. The CF x CW interaction effect was not significant and no depth main effect was found (Table 4-5).

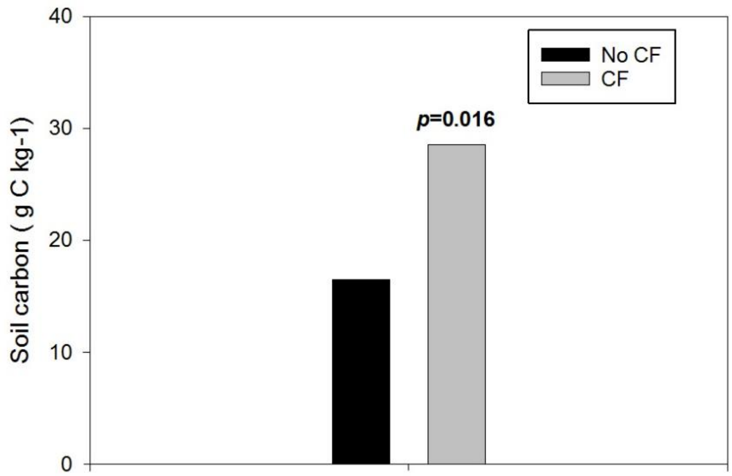

Figure 4-4. Significant main effect of CF on C concentration (g C kg^{-1}) for a juvenile loblolly pine plantation near Gainesville, FL.

IV.4.4 Soil total nitrogen

Total soil N followed the same trend as C for both the slash pine and loblolly pine plots. Depth effect was significant ($p < 0.05$) (Table 4-5), where total N was greater in the 0 - 20 cm than the 20 - 40 cm depth intervals (Table C-4). Although CFW had the highest total N in both the 0 - 20 cm and 20 - 40 cm depth interval (Table C-4), there was not a significant treatment effect (Table 4-5). For the past rotation's loblolly pine plots, total N tended to decrease with the depth interval, but not significantly.

Table 4-5. Statistical summary (p-values) of carry-over effect of species and treatment and effect of soil depth on soil C, N and P concentrations and C: N, C: P, and N: P ratios for a young loblolly pine plantation near Gainesville, FL.

		C	N	P	C: N	C: P	N: P
Effect	DF		*p*-value				
CF	1	**0.016**	**0.004**	**0.017**	0.883	0.779	0.327
CW	1	0.742	0.670	0.908	0.144	0.974	0.666
D (depth)	1	**0.017**	**0.034**	0.209	0.200	0.075	0.079
S (species)	1	0.798	0.082	0.497	**0.0003**	0.831	0.258
CF x CW	1	0.172	0.445	0.683	0.769	0.083	0.209
CF x D	1	0.384	0.688	0.808	0.804	0.930	0.740
CW x D	1	0.427	0.652	0.591	0.672	0.872	0.520
CF x CW x D	1	0.187	0.113	0.367	0.897	0.716	0.413
CF x S	1	0.468	0.106	0.750	0.640	0.263	0.084
CW x S	1	0.054	**0.045**	0.332	0.815	0.131	0.213
CF x CW x S	1	0.777	0.642	0.278	0.584	0.057	0.091
D x S	1	0.390	0.665	0.319	0.605	0.313	0.077

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table 4-5. Continued

Effect	DF	C	N	P	C: N	C: P	N: P
		p-value					
CF x D x S	1	0.479	0.438	0.651	0.564	0.817	0.608
CW x D x S	1	0.898	0.990	0.093	0.904	**0.024**	**0.008**
CF x CW x D x S	1	0.649	0.322	0.393	0.597	0.651	0.546

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05)

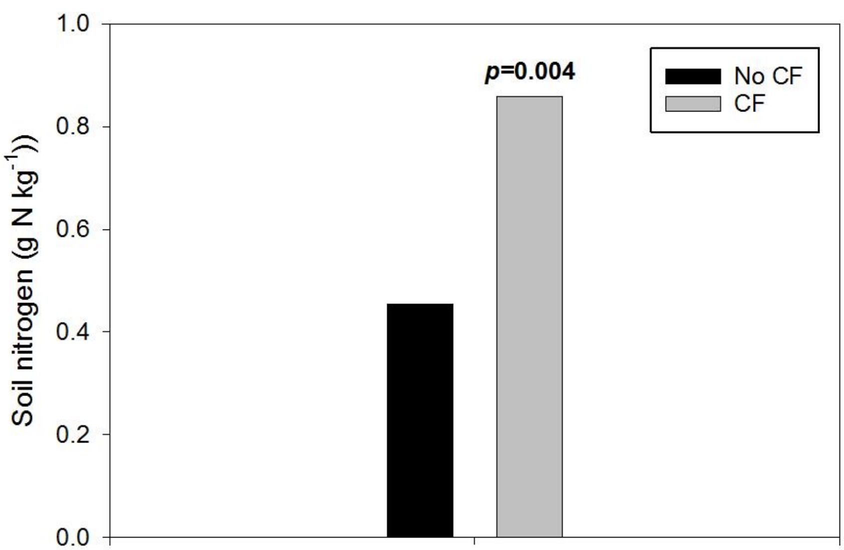

Figure 4-5. Significant main effect of CF on **N** concentration (g N kg^{-1}) for a juvenile loblolly pine plantation near Gainesville, FL.

So similar to total C, the CF treatment was significantly associated with increased total N in the 20 - 40 cm depth interval (Figure 4-5) and it had 15% more total N than in the 0 - 20 cm depth interval. For CFW, total N was 75% greater in the 0 - 20 cm than the 20 - 40 cm depth intervals (Table C-4). The interaction effect of CW and species (CW x S) was significant ($p < 0.05$), where CW had more N content for loblolly pine than slash pine.

IV.4.5 Soil phosphorus

Unlike soil total C and N, total P decreased with depth interval, albeit not significantly, for both the previous rotation's loblolly pine and slash pine plots (Table C-4). Fertilization had a significant carryover effect on total P for both previous rotation's species plots (Figure 4-6). The CF and CFW treatments had 50% and 20% greater total P in the 0 - 20 cm than 20 - 40 cm depth intervals relative to the control treatment, respectively (Table C-4). Like for total N, the CF treatment had lower total P in the 0 - 20 cm than the 20 - 40 cm depth intervals, but CFW had higher total P in the 0 - 20 cm than the 20 - 40 cm depth intervals for the loblolly pine plots (Table C-4). Total P was 86% greater and 38% lower in the 0 - 20 cm than the 20 - 40 cm depth intervals for the CFW and CF treatments, respectively (Table C-4).

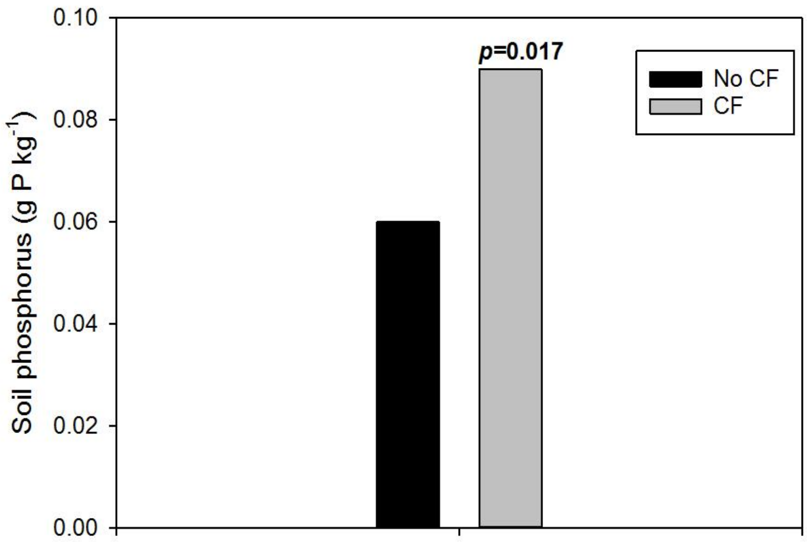

Figure 4-6. Significant main effect of CF on soil total phosphorus concentration (g P kg^{-1}) for a young loblolly pine plantation near Gainesville.

IV.4.6 Soil C: N, C: P, and N: P ratios

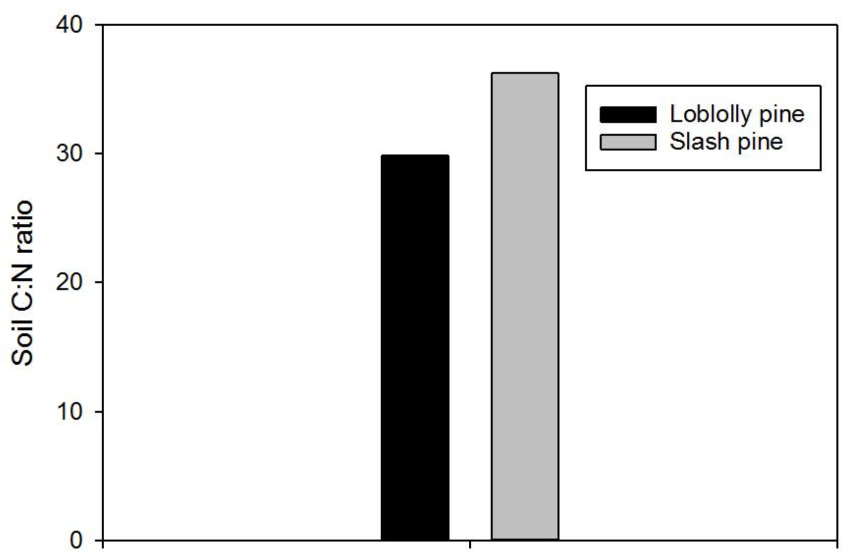

Figure 4-7 . Significant carryover effect of species on soil C: N ratio for a young loblolly pine plantation near Gainesville, FL.

Soil C: N, C: P, and N: P ratios decreased, although not significantly, with increasing soil depth interval for both plant species (Table C-4). In the 0 - 20 cm depth interval of the previous rotation's slash pine plots, the C: N ratios were 7-12% higher than the 20 - 40 cm ratios, with the CFW exhibiting the highest t ratios. The main effect of species was significant *(p*<0.05), where the C: N ratio was higher in the past rotation's slash pine than loblolly pine plots (Figure 4-7). The C: P ratios were approximately 10% greater in the 0 - 20 cm depth interval than in the 20 - 40 cm depth interval, with the CW treatment showing the highest ratios. The N: P ratios were slightly greater in the 0 - 20 cm depth interval than in the 20 - 40 cm depth interval, with treatments having lower ratios than the control for the 20 - 40 cm. Treatments did not significantly affect all ratios (*p*>0.05), but the interaction effect of the CW treatment, depth and species (CW x D x S) was significant *(p*<0.05) for the C: P and N: P ratios, where CW had significant greater ratios in the 20 - 40 cm depth interval than in the 0 - 20 cm depth interval for the past loblolly pine plots, while the opposite trend was observed in the previous rotation's loblolly pine plots. The CF x CW x S interaction effect was significant and indicated that the C: P ratios were higher in the CFW treatment than CF and CW treatments for both the 0 - 20 cm than the 20 - 40 cm depth interval and these ratios were greater in the past rotation's loblolly pine than slash pine plots, without the depth effect being significant. For the past rotation's loblolly pine plots, the C: N, C: P, and N: P ratios were 4%, 38% and 48 % higher in the 0 - 20 cm than the 20 - 40 cm depth intervals, respectively (Table C-3).

IV.4.7 Changes in soil extractable N and P through time.

IV.4.7.1 Effect of treatments on soil extractable N and P through time

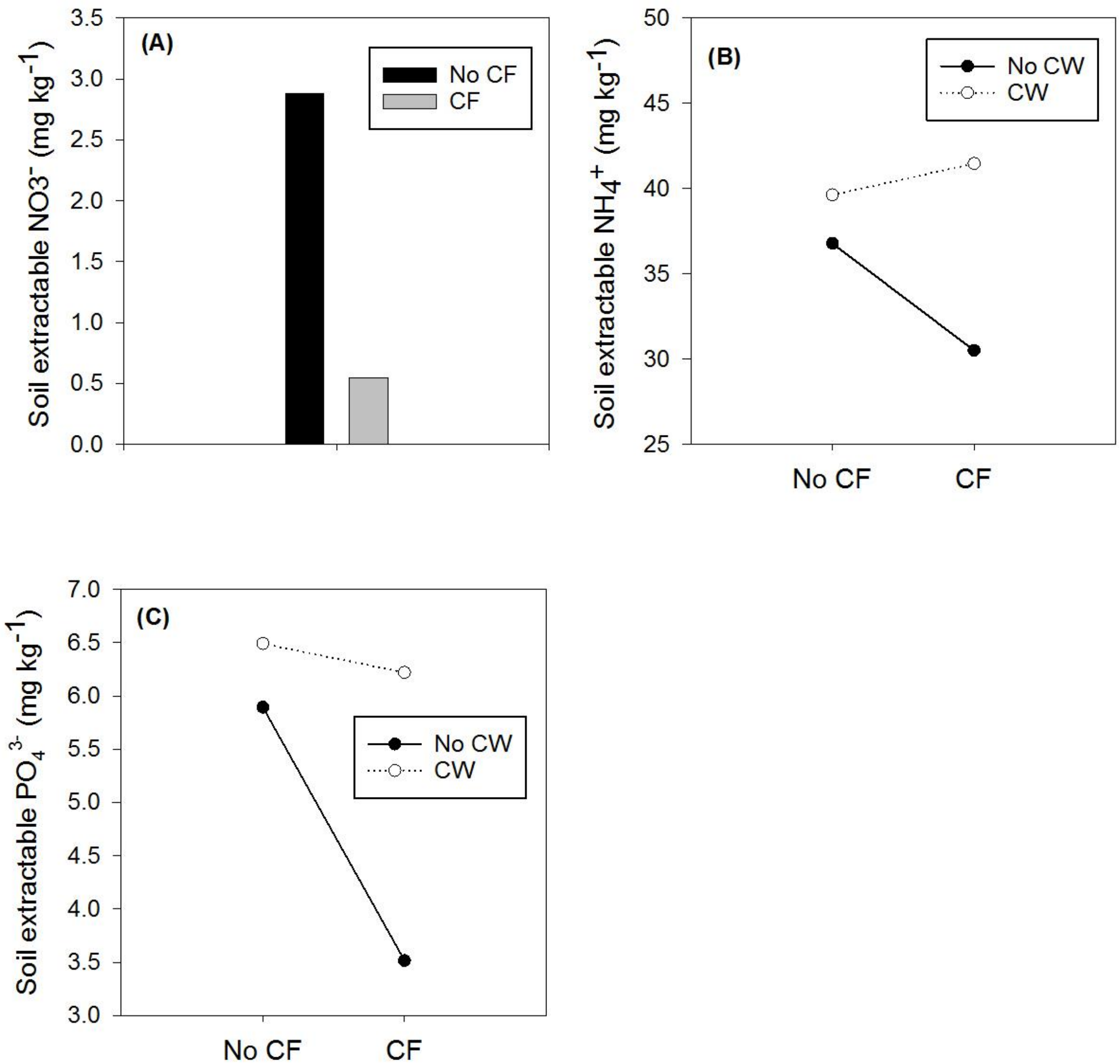

Figure 4-8. Significant CF main effect on (A) soil extractable nitrate, CF x CW interaction effect on soil (B) extractable ammonium and (C) extractable P for a young loblolly pine plantation near Gainesville, FL.

Extractable NH_4^+, NO_3^- and PO_4^{3-} concentrations varied with treatment, soil depth interval and duration of soil incubation for both loblolly pine and slash pine. The main effect of CF was significant and resulted in more than a 100% decrease in extractable NO_3^- concentrations in comparison to the control treatment (Figure 4-8A). The CF and CW main effects were significant for $NH4^+$ (Table 4-6), with CF resulting in a 15% increase of $NH4^+$ concentration relative to the CC treatment. Also, the CW main effect was A CFW x CW interaction effect (p<0.05) was significant and indicated a greater NH_4^+ concentration for the CFW than the CF and CW treatments (Figure 4-8B), with time of soil incubation (90 and 120 days) (Table C-5). The CF main effect was significant and increased the extractable P concentration by 41% in comparison to the CC treatment. The CW treatment showed the significant lowest extractable P concentration across depth intervals for both previous species and decreased it by 27% compared to the CC treatment (Table 4-6, Table C-6). A significant interaction effect (p<0.05) was found between CF and CW (Figure 4-8C) and indicated a decrease in P concentration in the CW and CFW treatments compared to the CF treatment for some time of extraction, suggesting a negative effect of the competition control on soil extractable P. More other significant main and interaction effects on extractable N and P are indicated in table 4-6.

Table 4-6. Statistical summary (p-values) of carry-over effect of species and treatment and effect of duration of incubation and soil depth on changes in soil extractable N and P concentrations for loblolly and slash pine plantation near Gainesville, FL

		[NH_4^+]	**[NO_3^-]**	**[PO_4^{3-}]**
Effect	DF	*p*-value	*p*-value	*p*-value
CF	1	**0.041**	**0.017**	**<.0001**
CW	1	**0.007**	0.249	**<.0001**
S	1	**<.0001**	0.079	**0.012**
D	1	0.180	**<.0001**	0.374
T (time)	4	**<.0001**	0.144	**0.019**
CF x CW	1	**0.043**	0.487	**0.0004**
CF x S	1	0.945	**0.031**	0.052
CW x S	1	0.255	**0.043**	0.216
CF x CW x S	1	0.990	0.462	0.560
CF x D	1	0.168	0.475	0.353
CW x D	1	0.897	0.455	0.601
CF x CW x D	1	0.507	0.827	0.958
S x D	1	0.760	0.675	0.355
CF x S x D	1	0.455	0.084	0.324
CW x S x D	1	0.171	0.171	0.255
CF x CW x S x D	1	0.996	0.497	0.666

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05)

Table 4-6. Continued

		$[NH_4^+]$	$[NO_3^-]$	$[PO_4^{3-}]$
Effect	DF	*p*-value	*p*-value	*p*-value
T x CF	4	0.734	0.544	0.823
T x CW	4	0.197	0.582	0.703
T x CF x CW	4	0.574	0.968	0.870
T x S	4	**<.0001**	**0.0004**	0.974
T x CF x S	4	0.853	0.552	0.999
T x CW x S	4	0.878	0.648	0.820
T x CF x CW x S	4	0.697	0.887	0.815
T x D	4	0.347	0.587	0.938
T x CF x D	4	0.682	0.734	0.977
T x CW x D	4	0.863	0.789	0.923
T x CF x CW x D	4	0.747	0.978	0.706
T x S x D	4	0.999	0.229	0.969
T x CF x S x D	4	0.957	0.803	0.884

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table 4-6. Continued

		$[NH_4^+]$	$[NO_3^-]$	$[PO_4^{3-}]$
Effect	DF	*p*-value	*p*-value	*p*-value
T x CW x S x D	4	0.877	0.887	0.865
T x CF x CW x S x D	4	0.748	0.674	0.994

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05)

The significant effect of species indicated significantly greater NH_4^+ and PO_4^{3-} concentrations in loblolly pine than slash pine (Figure 4-9A-B). The main effect of time (duration of soil incubation) was significant ($p<0.05$) and resulted in varitions in $NH4^+$ concentrations across treatments and soil depth intervals through time for both species. Likewise, the significant main effect of time indicated that extractable P concentrations increased from the beginning to 60 days of incubation and then decreased for the remainder of the incubation (90 and 120 days) across treatments, depth intervals and species (Table C-6). The effect of D (soil depth interval) was significant (Table 4-6) and indicated greater extractable NO_3^- concentrations in the 20 - 40 cm depth interval than the 0 - 20 cm depth interval for all species (Table C-5). The significant interaction effect of CF and species (CF x S) showed a decrease on NO_3^- for the loblolly pine relative to slash pine (Figure 4-9C). In contrast, a significant CW × S interaction reflected greater NO_3^- concentrations under the loblolly pine than slash pine in the CW treatment (Figure 4-9D). The significant effect of species indicated the greater extractable NH_4^+ concentration in loblolly pine than slash pine through time (Figure 4-9E). In contrast, there was a significant interaction effect of species and time where, NO_3^- was greater for loblolly pine than slash pine for some time during incubation (Figure 4-9F), highlighting N immobilization in the slash pine plots observed in all depth intervals.

IV.4.7.2 Effect of species on soil extractable N and P

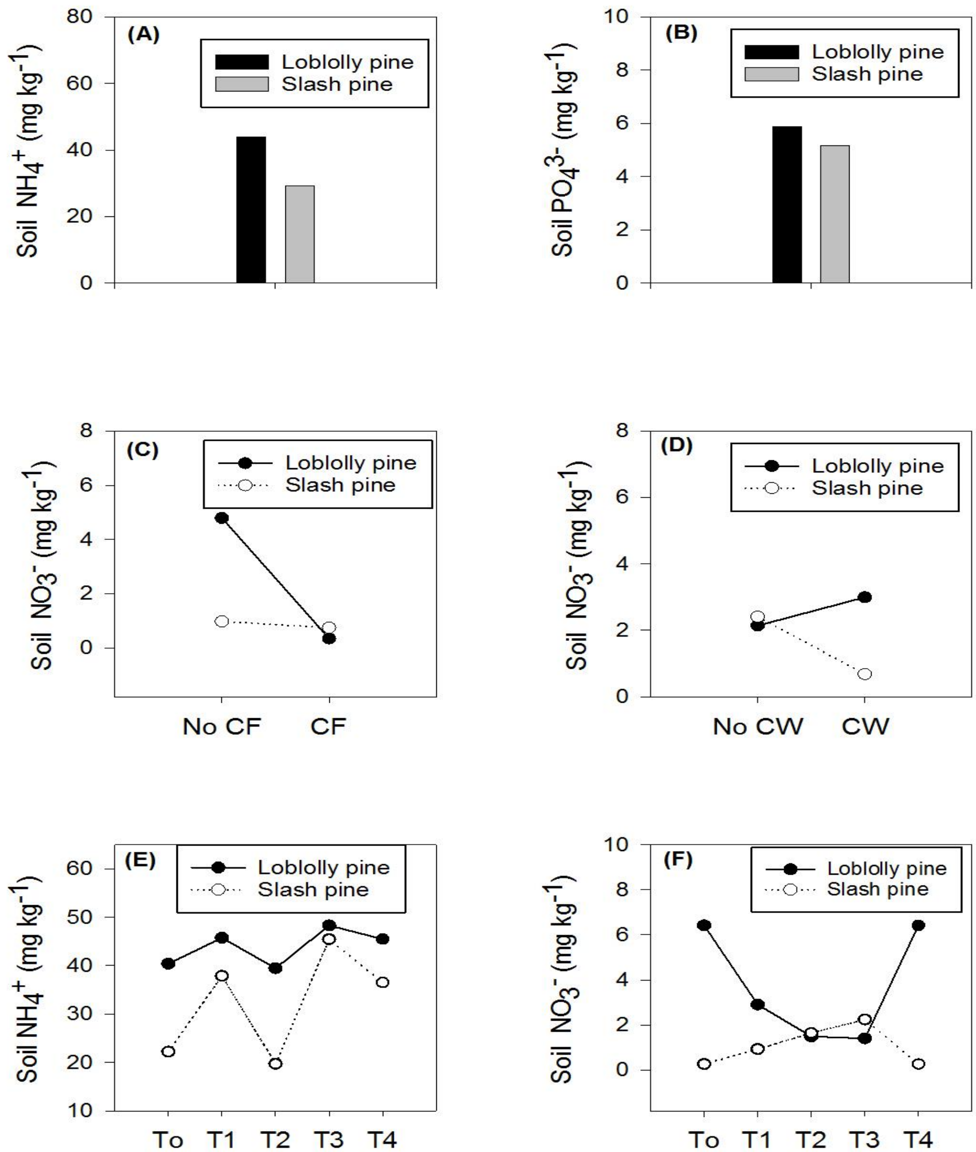

Figure 4-9. Significant S (species) main effect on (A) soil NH_4^+ and (B) soil PO_4^{3-}, CF x S interaction effect on (C) soil NO_3^-, CW x S interaction effect on (D) soil NO_3^-, S x T interaction effect on (E) soil NH_4^+ and (F) soil NO_3^- for a previous loblolly pine and slash pine plantation near Gainesville, FL.

Table 4-7. Spearman's correlation coefficients among soil properties and extractable N and P from a slash pine plantation near Gainesville, FL.

Depth interval (cm)		Time	pH	[C]	[N]	[P]	C:N	C:P	N:P	Extractable N ($NH_4^+ + NO_3^-$)
0-20										
	[C]	--	-0.66**							
	[N]	--	-0.67**	0.97**						
	[P]	--	-0.50*	0.88**	0.86**					
	C:N	--	-0.39*	0.80**	0.67**	0.63**				
	C:P	--	-0.52*	0.56**	0.55**	0.14	0.65**			
	N:P	--	-0.46*	0.24*	0.31	-0.20	0.16	0.85**		
	Extractable N ($NH_4^+ + NO_3^-$)	0.15	-0.32*	0.39	0.35*	0.31*	0.33*	0.26	0.12	
	Extractable PO_4^{3-}	-0.12	-0.15	0.23	0.24	0.34*	0.18	-0.01	-0.11	0.12

** p <0.01 * p < 0.05

Table 4-7. Continued

Depth interval (cm)		Time	pH	[C]	[N]	[P]	C:N	C:P	N:P	Extractable N ($NH_4^+ + NO_3^-$)
20-40										
	[C]	--	-0.74**	--						
	[N]	--	-0.70**	1.00**						
	[P]	--	-0.68**	0.88**	0.89**					
	C:N	--	-0.87**	0.78**	0.73**	0.55**				
	C:P	--	0.13	0.04	0.02	-0.39	0.25			
	N:P	--	0.58**	-0.34*	-0.33	-0.65**	-0.25	0.87**		
	Extractable N ($NH_4^+ + NO_3^-$)	0.05	-0.56**	0.39*	0.38*	0.58**	0.38*	-0.45*	-0.62**	
	Extractable PO_4^{3-}	-0.02	-0.18	0.13	0.12	0.20	0.15	-0.11	-0.19	0.26

** p <0.01 * p < 0.05

The Spearman's correlation coefficients among soil properties and extractable N and P are summarized in the tables 4-7 and 4-8. Briefly, in the 0-20 cm depth interval of the previous slash pine plots, total N was negatively correlated with pH (r = -0.67), but positively with extractable N (r = 0.35), total P concentration (r = 0.86), C: N ratio (r = 0.67) and C: P ratio (r =0.55) (Table 4-7). In the 20-40 cm depth interval, total N negatively correlated with pH (r = -0.70), but positively correlated with C (r = 1.00), extractable N (r = 0.38), P concentration (r = 0.89) and C: N ratio (r = 0.73) (Table 4-7) for the previous rotation's slash pine plots. For the past loblolly pine plots (Table 4-8), N concentration was negatively correlated with pH (r = - 0.75), extractable N (r = -0.30), extractable P (r = -0.28), C: N ratio (r = - 0.37, but positively correlated with P concentration (r = 0.47) and ratios of C: P ratio (r = 0.60) and N: P (r = 0.63) in the 0-20 cm depth interval. In the 20-40 cm depth interval, N concentration also positively correlated with P concentration (r = 0.96) and N: P ratio (r = 0.51).

For the past slash pine plots, P concentrations were negatively correlated with pH (r = -50), but positively correlated with C (r = 0.88), C: N ratio (r = 0.63), extractable N (r = 0.31) and phosphate (r = 0.34) for the 0 - 20 cm depth interval (Table 4-7). In the 20 - 40 cm depth interval, total P negatively correlated with pH (r = - 0.68), N:P ratio (r = -0.65), but positively correlated with C (r = .88), C:N (r = 0.55) and extractable N (r = 0.58). Unlike N, total P concentrations were negatively correlated with the ratios of C: P (r = -0.35) and N: P (r = -0.35) in the 0 - 20 cm depth interval, but positively correlated with N: P ratio (r = 0.32) in the 20 - 40 cm depth interval for the loblolly pine plots (Table 4-8).

Table 4-8. Spearman's correlation coefficients among soil properties and extractable N and P from a loblolly pine plantation near Gainesville, FL.

Depth interval (cm)		Time	pH	[C]	[N]	[P]	C:N	C:P	N:P	Extractable N (NH_4^+ + NO_3^-)
0-20 cm										
	[C]	--	-0.77**							
	[N]	--	-0.75**	0.98**						
	[P]	--	-0.68**	0.50*	0.47*					
	C:N	--	0.19	-0.20	-0.37*	-0.01				
	C:P	--	-0.15	0.62**	0.60**	-0.35**	-0.09			
	N:P	--	-0.16	0.63**	0.63**	-0.35*	-0.23	0.99**		
	Extractable N (NH_4^+ + NO_3^-)	0.12	-0.20	-0.26	-0.30*	0.08	0.24	-0.43*	-0.46*	
	Extractable PO_4^{3-}	-0.09	0.23	-0.32*	-0.28	0.11	-0.06	-0.44*	-0.41*	0.02

** p <0.01 * p < 0.05

Table 4-8. Continued

Depth interval (cm)		Time	pH	[C]	[N]	[P]	C:N	C:P	N:P	Extractable N ($NH_4^+ + NO_3^-$)
20-40 cm										
	[C]	--	-0.76**							
	[N]	--	-0.64**	0.97**						
	[P]	--	-0.60**	0.97**	0.96**					
	C:N	--	-0.16	-0.08	-0.13	-0.12				
	C:P	--	-0.64**	0.23	0.16	0.00	0.05			
	N:P	--	-0.62**	0.47*	0.51*	0.32*	0.23	0.76**		
	Extractable N ($NH_4^+ + NO_3^-$)	-0.03	-0.27	0.18	0.17	0.17	-0.49*	0.04	-0.03	
	Extractable PO_4^{3-}	-0.09	0.09	0.12	0.19	0.16	-0.50*	-0.11	-0.17	0.29*

** p <0.01 * p < 0.05

IV.5. Discussion

Forest scientists have long investigated how tree species differ in their effects on ecosystem carbon (Vesterdal et al. 2013) and nutrient cycles (Stone and Gibson 1975, Binkley and Giardina 1998). With increasing use of plantation silviculture that trends toward planting a single species (South and Harper 2016), species effects questions have been expanded to how composition interacts with silvicultural practices. This study builds on past studies from the same research site that, over a 26-year rotation, contrasted loblolly pine and slash pine growth response to silvicultural practices (Colbert et al. 1990, Martin and Jokela 2004, Jokela et al. 2010), and differences in nutrient cycling (Polglase et al. 1992a, Vogel et al. 2011). In an examination of the C and N pools at the end of rotation, Vogel et al. (2011) found no species level main effects for either element, but did show that significant species interactions with silviculture (fertilization or competition control) were restricted to C and N in pine tissues. These interactions reflected that relative to loblolly pine, slash pine produced more biomass with competition control and less biomass under fertilization (Jokela et al. 2010). However, in the current study on the P cycle, species main effects were evident for the forest floor and roots >2 mm, and reflected that slash pine stored less P than loblolly pine in these pools. The forest floor results suggest that in detrital pools, the species differ in how they cycle P, but not in how they cycle C and N (Vogel et al. 2011).

The differences between species in forest floor P were large enough to grow next rotation's stands of loblolly pine or slash pine plantations. A possible reason for these species differences could be related to litter fall chemistry. Loblolly pine litter has been reported to have higher nutrient (N and P) concentrations than slash pine (Polglase et al. 1992b, Dicus and Dean 2008), resulting in higher N and P mineralization rates in stands of loblolly pine than in slash pine. Loblolly pine also allocates more biomass to foliage growth than slash pine (Colbert et al. 1990), which would also increase the amount of P cycling through the forest floor. These inherent differences between the species would be greater where competition was eliminated, which may be why loblolly pine in the 33 - 66 cm soil layers had greater P in the W plots than slash pine. This interval included the Bh horizon, and given that loblolly pine roots were also higher in P, the Bh under loblolly pine may have received both more leaching from the forest floor and direct P input from roots that then complexed with the humic-Fe and -Al oxides (Villapando and Graetz 2001).

An additional question in this research was whether these species difference in P pools would translate to difference in growth or nutrient availability in the next rotation. The second-rotation IMPAC II study has only loblolly pine planted in the untreated carry-over treatments (previously slash pine) and in actively managed treatments (previously loblolly pine) that are receiving similar levels of silviculture as the first rotation. Given this design, the control plots are the only ones that can be compared for differences caused by species, but they did not differ in growth after three years (Subedi et al. 2014), suggesting there is no carry-over effect of species selection. At the beginning of the IMPAC II rotation, there was also no difference in extractable P from the slash than loblolly pine forests (now carry-over plots). The C: P ratios of these soils suggest a high potential for microbial immobilization of P (Pastor et al. 1984); a phenomenon previously observed for P at this site (Polglase et al. 1992a) and likely why P concentration often decreased in this study's repeated extractions (Table C-7). Negative correlations between extractable N and P and the C: N and C: P ratios across treatments suggested these ratios reflected a high immobilization potential (Table 4-7). With the slash pine stands having higher C: P ratios than the loblolly pine forests, chemical characteristics of soil organic matter could have been more important to early nutrient availability than was total pool size. Moreover, the high C:N ratio in both the loblolly and slash pine forest would also favor immobilization of N rather than mineralization (Springob and Kirchmann 2003), highlighting that despite changes in nutrient pools caused by species selection or silviculture, active management that increases nutrient availability (e.g. fertilization) may be required to increase forest productivity.

Tree growth in the second rotation was increased by fertilization and was slightly depressed where only competition control had been previously used (Subedi et al. 2014); suggesting that past silviculture had much greater effects on subsequent growth than did species effects. In a similar study, the carry-over effects of fertilization and competition control were also significant effects on next rotation tree growth (Chapter III). The effect of silviculture on IMPAC II tree growth likely reflected that fertilization increased both forest floor N (Vogel et al. 2011) and P (Table 4-2) pools. In contrast, the species effect was only significant for P (Tables 4-2 and 4-3). Moreover, the changes in N and P could have mirrored changes in multiple elements as the fertilized plots received a suite of macro- and micronutrients, and tree growth was correlated with exchangeable P, Zn and Cu across all carry-over treatments (Subedi et al. 2014). Studies suggest that multiple elements may limit productivity on Florida Spodosols (Jokela et al. 1991, Vogel and Jokela 2011). The dynamics of multiple elements may be particularly relevant in areas where competing understory plants are prevalent, as understory species can accumulate more nutrients than pine during the first few years of stand development (Subedi et al. 2014).

IV.6. Conclusions

Species selection affected P dynamics in this study, as loblolly pine and slash pine differed in how they directly affected P in some pools and interacted with competition control. However, no species effects were evident in second rotation growth differences. More impactful were the positive effects of fertilization and to a lesser degree, the negative effects of weed control early in next rotation growth. The trends in next rotation growth corresponded with P pool trends, while the trends in extractable N did not support the hypothesis that this element limited early productivity. The high C: N and C: P ratios early in the rotation of these plantations suggest they suffer from a high N and P immobilization potential in the soil and that they require some nutritional assistance to reach potential growth, especially if competition control was the only silvicultural treatment in the previous rotation.

CHAPTER V

SUMMARY AND CONCLUSIONS

The managed pine stands of the southeastern United States are some of the most intensively managed forests in the world and are important components of the regional economy. Like forests generally, managed forests are also important for mitigating increases in atmospheric carbon dioxide. Carbon dioxide and other greenhouse gas emissions are widely believed to be the main drivers of climate change and global warming. The global human population continues to increase exponentially while forestlands has decreased due to land conversions and urbanization. Thus, intensive forest management systems will play an important role in different parts of the world for meeting the high demand for forest products and other related ecosystem services. The increasing human population will also increase the energy demand which then affects fertilizer and competition control prices, making silvicultural practices more expensive. Therefore, the efficient use of fertilizer that can increase forest productivity both in current and future rotations could increase the return on a fertilizer investment both monetarily and in terms of C mitigation. Yet, few studies have examined how silvicultural treatments used in one rotation affect subsequent growth and C, N, and P dynamics in the next rotation. Therefore, the purpose of this study was to determine the effect of species selection, fertilization, competition control and the combined application of these treatments and their carry-over effects on tree growth and C, N and P dynamics in the loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Engelm.) plantations of north-central Florida. This study used the Intensive Management Practices Assessment Center (IMPAC) and G8 experimental sites both located in north-central Florida to examine the effects of silvicultural practices on tree growth and productivity over the course of a rotation (25 or 26 years) and their carry-over effects on the subsequent rotation's growth and productivity.

The G8 experiment was one of 25 G-series of experimental sites established in 1987 by the University of Florida's Cooperative Research in Forest Fertilization program in cooperation with Auburn University's Silviculture Herbicide Cooperative to evaluate the main effects and interactions of fertilizer and competition control treatments applied at establishment and at mid-rotation on the potential growth of managed pine forests (Johnson 1992, Jokela et al. 2000). The original experiment was established as a randomized complete block design with six treatments and three blocks: Control (C), fertilization with diammonium phosphate (F_{DAP}), competition or 'weed' control (W), fertilization with diammonium phosphate mixed with competition control ($F_{DAP}W$), fertilization with triple superphosphate (F_{TSP}), and fertilization with triple superphosphate plus competition control ($F_{TSP}W$). The second rotation was overlaid on the first rotation's plots where the carry-over plots (CC, CF, CW, and CFW) did not receive any additional treatments (fertilizer or competition control) while the retreated plots (F and FW) received fertilizer either alone or with competition control treatments.

At the end of rotation, fertilization-only did not increase pine biomass or C accumulation, unless it was combined with competition control. This non-response to fertilization-alone was likely due to the site having relatively high background fertility. Biomass C accumulation was moderately increased by fertilization combined with competition control. These results highlight the additive effects of these treatments in alleviating nutrient deficiency and competition to optimize pine productivity. Similar to C accumulation, when N and P pools in vegetation were significantly increased, it occurred when fertilization plus competition control were the treatment. In contrast, fertilization alone did increase N and P accumulation in forest floor and soil intervals, although there was no significant increase in C accumulation, indicating a decoupling of the C and

N and P dynamics. Contrary to fertilization, the W significantly decreased the P in forest floor (Oi and Oe+Oa) layers. This decrease may likely reduce P availability in the next rotation.

Inorganic forms of soil N and P were extracted once, and fertilization increased PO_4^{3-} throughout the soil horizons, while the competition control significantly decreased both NH_4^+ and NO_3^- concentrations but often increased them where fertilizer was also added. Variation in litter chemistry was thought to influence these differences between N and P response to silvicultural treatments where the litter was derived only from pine tissues for the competition control plots and pine, woody and herbaceous understory plants for the fertilized-only plots.

Treatments significantly increased N and P, and soil extractions from deeper portions of the profile suggested nutrient downward movement. It is uncertain whether this movement indicated the nutrient losses from the ecosystem because soil sampling was limited to 1 m and did not reach the argillic horizon, where a higher exchange capacity would most likely hold N and P. Another potential way that P was held from leaching could be its binding with organic matter and Al and Fe sesquioxides that are dominant in the spodic horizon found between the 20 - 50 cm and 50 - 100 cm depth intervals. However, it remains unclear whether P that moved to deeper soil will be accessible to plants when roots grow into the deeper soil layers.

Comparison of forest growth between the first and second rotation at G8 site was used to investigate changes in productivity and nutrient dynamics in response to previous treatments. Pine growth in both the carryover and retreated treatments of the second rotation were much greater than the growth of the first rotation. This higher growth in the second rotation was likely due to the improved silvicultural practices, genetic selection of seedlings, bedding techniques, and diseases control and environmental factors like increase in mean precipitation and CO_2 concentration. In the carryover plots, the lowest growth was found in the W treatment and corresponded to lower

NH_4^+, indication that the early rotation growth was limited by N. For the retreated plots, fertilization with N, P, K, and a suite of micronutrients significantly increased the growth (DBH) while in the first rotation, the effect of fertilizer (only with N and P) was not significant. This accelerated growth with a mixture of macro- and micronutrients indicated that nutrients other than N and P are limiting to pine growth at this study site. N mineralization potential was the greatest in the competition control plots due to the decreased bioavailable C that it was related to the dominance of pine litter, reducing N immobilization in favor of N mineralization. Notable was the P immobilization at 20 - 50 cm likely due to the in-situ soils that were near saturation at the time of collection, suggesting that the microbial population was suppressed in situ. Likely, the decrease in ammonification and increase in nitrification with soil depth may support the fact that in situ conditions suppressed the microbial populations responsible for nitrification.

The IMPAC experiment was established by the University of Florida and United States Forest Services in 1983 to evaluate the effects of intensive management practices on southern pine forests productivity (Jokela et al. 2010). The original study employed a 2x2x2 factorial experiment consisting in combination of species (loblolly and slash pines) and treatments replicated in three blocks (C: control, F: fertilizer only, W: weed control, FW: fertilizer plus weed control) completely randomized in each species as whole plot; organized in a split-plot experimental design. The second rotation's study was consisted of two randomized complete block designs (RCBD) with four treatments (CC, CF, CW and CFW) for untreated carryover design and four treatments (C, W, RF and RFW) completely randomized in three replicate blocks. The untreated carry-over plots were established on the previous slash pine plots and the actively re-fertilized plots were established on the previous loblolly pine plots.

At the end of first rotation of IMPAC, the effect of species was significant for P in organic horizons, with greater P in loblolly pine than slash pine horizons. Litter fall chemistry had previously been observed to differ between the species with loblolly pine having higher nutrient (N and P) concentrations and also allocates more biomass to foliage growth than slash pine. The difference between species was the most pronounced in the competition control treatments. This may be why loblolly pine accumulated in the 33 - 66 cm soil layers greater P in the W plots than slash pine. This higher P accumulation may be was a sum of P input from roots and the leaching from forest floor that were complexed with the humic-Fe and -Al oxides in the Bh horizon present in that soil interval. Uncertain was whether the species selection and treatments effects would carry on to the second rotation.

At the beginning of the next rotation, the effect of species selection was not evident in soil total C, N, and P nutrients but species did have a significant effect on extractable N and P where loblolly pine had greater extractable NH_4^+ and PO_4^{3-} than slash pine and interacted with competition control to increase extractable NO_3^-. In contrast to species effects, fertilization consistently increased next rotation soil C, N and P concentrations, suggesting that the positive effect of fertilization used in the past rotation carried on to the second rotation. Also, past fertilization increased extractable NO_3^- and interacted with completion control to increase extractable NH_4^+ and PO_4^{3-}.

These results suggest that species effects may be significant but silviculture will have a greater effect on site productivity potential. Collectively, these results suggest that while ecosystem nutrient dynamics response to silvicultural treatments are related to site background fertility where the high site fertility decreases the fertilization effect on pine growth. This would raise the question of whether these effects will carry-on to the next rotation. Therefore, subsequent fertilization prescriptions could consider the previous rotation's fertility level in order to improve the efficiency use of fertilizer. A slight negative carryover effect of past competition control may suggest the application of a more complete fertilizer mix of micro- and macro elements and competition control in the second rotation to enhanced productivity as some nutrient limit growth in the research sites. Additionally, species selection would be crucial to productivity as they differently affect inter-rotational nutrient dynamics.

Results of this study will contribute fundamental knowledge regarding the effects of intensive forest management practices on inter-rotational productivity and sustainability and may be accessible to stakeholders such as state, federal, and forest industry groups or other private forestland owners who wish to sustainably manage plantations. These stakeholders will use this information to adjust management prescriptions that would ultimately save them money, increase forest growth, and reduce nutrient losses from forest management practices. In addition, knowledge from the results of this study may be useful to scientists coupling C, N and P to modeling regional biogeochemical cycles determining a forest's potential to serve as a carbon sink to mitigate regional and global climate change.

I identified few limitations in this study to better explain some findings. Soil sampling was limited to 40 cm and 50 cm for IMPAC II and SSPS sites, respectively because deeper soils were excessively wet due to the raised water table and soil could not be removed. Deeper soils should be sampled at these sites and further research on nutrient dynamics throughout the soil profile is recommended. Also, an analysis of organic matter chemistry or/and microbial function is recommend to better understand the effects of silvicultural practices on differences between N and P in extractable elements. At the end of G8 rotation, exchangeable P movement to deep soils was observed. A further assessment of P availability to bigger trees in deeper soils is recommended. This would require the soil sampling up to the spodic and argillic horizons to assess the P retention in the soil profile.

The high C: N and C: P ratios early in the rotation of these plantations suggest they suffer from a high N and P immobilization potential in the soil. A complete fertilizer mix is required and assessment of its effect on potential growth is recommended.

Nutrient supply rates measurement using ion exchange membranes at mid-rotation is recommended to understand the fertilizer prescription' rates that are needed throughout the end of rotation. Also, correlations between aboveground loblolly pine biomass and soil nutrient supply rates would need to be assessed.

Results of this study suggest the beds have a positive influence on soil N and P availability early in rotation. Assessment of soil bedding effects on depth wise change in nutrient availability is recommended for these poor drained soils to maintain productivity.

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APPENDIX A

STATISTICAL RESULTS (MEAN VALUES): G8 SITE

Table A-1. Mean (± SE) C pools (Mg C ha^{-1}) in aboveground vegetation, forest floor, and soil for a 25-year-old loblolly pine stand near Palatka, FL fertilized with diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP}), weed control (W), and fertilization combined with weed control (F_{DAP} W and F_{TSP} W).

	Aboveground components				Forest floor	Root	Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem wood	Oi+ Oe+Oa	Root	0-10	10-20	20-50	50-100
C	4.3	12.3	15.0	105.7	11.9	25.7	28.8	15.6	12.1	63.9
	(0.4)	(0.4)	(1.4)	(5.6)	(1.4)	(1.3)	(2.9)	(2.9)	(1.7)	(7.2)
W	4.7	13.7	16.9	119.0	8.9	28.7	30.9	18.0	14.3	59.6
	(0.5)	(1.4)	(2.1)	(13.2)	(2.2)	(3.3)	(2.8)	(2.8)	(3.2)	(4.0)
F_{DAP}	4.2	12.4	15.2	105.5	10.7	26.7	28.2	12.5	9.6	66.3
	(0.4)	(0.8)	(1.7)	(8.9)	(1.2)	(2.2)	(5.2)	(1.2)	(2.3)	(3.9)

Table A-1. Continued

	Aboveground components				Forest floor	Root	Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem wood	Oi+ Oe+Oa	Root	0-10	10-20	20-50	50-100
F_{DAP} W	5.1	14.4	18.4	126.7	10.4	35.4	30.2	18.4	15.4	68.2
	(0.1)	(0.1)	(0.3)	(1.1)	(0.8)	(0.3)	(2.7)	(2.5)	(2.1)	(9.7)
F_{TSP}	4.2	12.7	14.9	109.3	11.0	26.9	28.0	18.4	15.4	48.8
	(0.2)	(0.9)	(0.9)	(7.6)	(1.6)	(1.9)	(1.6)	(3.8)	(1.9)	(8.1)
F_{TSP} W	5.3	15.0	19.1	131.5	11.5	34.1	33.5	19.5	22.4	69.0
	(0.6)	(0.9)	(2.0)	(9.5)	(2.1)	(2.3)	(6.1)	(4.1)	(7.0)	(9.2)

Table A-2. Mean (± SE) N concentration (g kg^{-1}) in aboveground vegetation, forest floor, and soil for a 25-year-old loblolly pine stand near Palatka, FL fertilized with diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP}), weed control (W), and fertilization combined with weed control (F_{DAP} W and F_{TSP} W).

	Aboveground components				Forest floor	Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem-wood	Oi+Oe+Oa	0-10	10-20	20-50	50-100
C	11.3	1.0	1.4	0.4	3.9	0.95	0.44	0.13	0.29
	(0.51)	(0.08)	(0.01)	(0.06)	(0.4)	(0.07)	(0.07)	(0.02)	(0.03)
W	10.6	1.1	1.3	0.3	3.7	1.02	0.48	0.14	0.25
	(0.49)	(0.13)	(0.01)	(0.03)	(0.4)	(0.08)	(0.07)	(0.01)	(0.01)
F_{DAP}	10.9	1.3	1.3	0.3	4.0	0.91	0.41	0.13	0.30
	(0.51)	(0.07)	(0.01)	(0.03)	(0.5)	(0.06)	(0.07)	(0.02)	(0.03)

Table A-2. Continued

	Aboveground components				Forest floor	Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem wood	Oi+Oe+Oa	0-10	10-20	20-50	50-100
F_{DAP} W	11.0	1.4	1.5	0.5	4.4	1.01	0.48	0.15	0.30
	(0.26)	(0.02)	(0.01)	(0.02)	(0.4)	(0.08)	(0.06)	(0.02)	(0.03)
F_{TSP}	11.5	1.5	1.2	0.4	4.8	0.80	0.55	0.17	0.32
	(0.74)	(0.03)	(0.01)	(0.04)	(0.3)	(0.03)	(0.06)	(0.03)	(0.09)
F_{TSP} W	11.7	1.2	1.2	0.3	4.2	1.13	0.57	0.22	0.31
	(0.25)	(0.04)	(0.00)	(0.04)	(0.6)	(0.19)	(0.08)	(0.03)	(0.03)

Table A-3. Statistical summary (ρ values) for main and interaction effects of treatments on N concentration (g kg^{-1}) in aboveground vegetation, forest floor, and soil for a 25-year-old loblolly pine (*Pinus taeda*) stand in Palatka, FL treated with diammonium phosphate (F_{DAP}), triple superphosphate (F_{TSP}), weed control (W), and fertilization combined with weed control (F_{DAP}W and F_{TSP} W).

	Aboveground biomass				Forest floor
Effect	Foliage	Bark	Branch	Stem wood	Oi+Oe+Oa
F_{DAP}	0.937	0.063	**0.017**	0.233	0.331
W	0.502	0.169	0.914	0.107	0.845
F_{DAP} x W	0.383	**0.016**	0.344	**0.016**	0.466
F_{TSP}	0.241	**0.009**	**0.046**	0.760	0.091
W	0.572	0.065	0.886	0.501	0.295
F_{TSP} x W	0.380	0.614	0.401	0.653	0.612

DF =1 for all main and interaction effects

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table A-4. Mean (± SE) N accumulation (kg N ha^{-1}) in aboveground vegetation, forest floor and soil for a 25-year-old loblolly pine stand near Palatka, FL fertilized with diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP}), weed control (W), and fertilization combined with weed control (F_{DAP} W and F_{TSP} W).

	Aboveground components				Forest floor	Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem wood	Oi + Oe+Oa	0-10	10-20	20-50	50-100
C	116	31.2	25.7	261.5	446	1010	562	533	2010
	(14.1)	(1.7)	(5.5)	(15.3)	(50)	(72)	(88)	(69)	(233)
W	117	35.2	27.8	297.6	378	1086	625	565	1816
	(12.3)	(4.6)	(3.7)	(41.4)	(63)	(81)	(94)	(48)	(108)
F_{DAP}	95	34.5	22.8	293.2	512	973	534	528	2167
	(11.6)	(2.5)	(6.3)	(24.7)	(67)	(61)	(85)	(89)	(187)

Table A-4. Continued

	Aboveground components				Forest floor	Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem wood	Oi + Oe+Oa	0-10	10-20	20-50	50-100
F_{DAP} W	130	40.1	32.8	341.8	485	1079	614	626	2145
	(5.6)	(3.3)	(4.8)	(27.4)	(44)	(86)	(77)	(65)	(238)
F_{TSP}	103	35.9	25.0	300.7	556	861	710	687	2453
	(9.5)	(1.6)	(5.8)	(12.6)	(43)	(29)	(81)	(127)	(604)
F_{TSP} W	130	44.2	30.9	376.1	540	1204	952	887	2215
	(12.9)	(3.7)	(3.5)	(35.3)	(73)	(98)	(70)	(140)	(233)

Table A-5. Statistical summary (ρ values) for main and interaction effects of treatments on N accumulation (kg N. ha[-1]) in aboveground vegetation, forest floor, and soil for a 25-year-old loblolly pine (*Pinus taeda*) stand in Palatka, FL treated with diammonium phosphate (F_{DAP}), triple superphosphate (F_{TSP}), competition control (W), and fertilization combined with weed control (F_{DAP}W and F_{TSP} W).

	Aboveground biomass				Forest floor	Soil depth interval (cm)			
Effect	Foliage	Bark	Branch	Stem wood	Oi+Oe+Oa	0-10	10-20	20-50	50-100
F_{DAP}	0.272	0.065	**0.020**	**0.045**	0.119	0.712	0.797	0.943	**0.022**
W	0.307	0.127	**0.031**	**0.020**	0.382	0.223	0.349	0.108	0.402
F_{DAP} x W	0.468	0.592	**0.028**	**0.014**	0.700	0.787	0.055	0.540	0.478
F_{TSP}	0.083	0.860	0.086	0.654	**0.021**	0.869	0.140	**0.038**	0.053
W	0.146	0.169	0.447	0.699	0.446	0.095	0.334	0.255	0.400
F_{TSP} x W	0.248	0.730	0.460	0.543	0.637	0.255	0.568	0.461	0.967

DF =1 for all main and interaction effects

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table A-6. Mean (±SE) P concentration (g kg^{-1}) in aboveground vegetation, forest floor, and soil for a 25-year-old loblolly pine stand near Palatka, FL treated with fertilization (diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP})), weed control (W), and fertilization combined with weed control (F_{DAP} W and F_{TSP} W).

	Aboveground components				Forest floor		Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem-wood	Oi	Oe+Oa	0-10	10-20	20-50	50-100
C	0.99	0.17	0.059	0.047	0.38	0.29	0.024	0.011	0.0047	0.025
	(0.01)	(0.00)	(0.007)	(0.009)	(0.028)	(0.023)	(0.002)	(0.001)	(0.0008)	(0.004)
W	0.84	0.17	0.062	0.040	0.37	0.27	0.029	0.016	0.0054	0.030
	(0.09)	(0.00)	(0.010)	(0.005)	(0.018)	(0.017)	(0.002)	(0.003)	(0.0013)	(0.007)
F_{DAP}	1.05	0.19	0.062	0.041	0.48	0.36	0.046	0.016	0.0049	0.019
	(0.03)	(0.01)	(0.003)	(0.002)	(0.019)	(0.023)	(0.018)	(0.002)	(0.0010)	(0.002)

Table A-6. Continued

	Aboveground components				Forest floor		Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem wood	Oi	Oe+Oa	0-10	10-20	20-50	50-100
F_{DAP} W	1.01	0.17	0.091	0.045	0.42	0.33	0.033	0.016	0.0051	0.019
	(0.01)	(0.02)	(0.011)	(0.002)	(0.014)	(0.033)	(0.003)	(0.002)	(0.0007)	(0.003)
F_{TSP}	0.85	0.15	0.045	0.033	0.49	0.37	0.023	0.014	0.0062	0.020
	(0.08)	(0.01)	(0.005)	(0.004)	(0.016)	(0.012)	(0.002)	(0.003)	(0.0008)	(0.002)
F_{TSP} W	1.19	0.18	0.060	0.048	0.45	0.31	0.031	0.015	0.0077	0.017
	(0.05)	(0.00)	(0.011)	(0.002)	(0.015)	(0.026)	(0.004)	(0.003)	(0.0012)	(0.003)

Table A-7. Statistical summary (ρ values) for main and interaction effects of treatments on P concentration (g kg^{-1}) in aboveground vegetation and forest floor for a 25-year-old loblolly pine (*Pinus taeda*) stand in Palatka, FL treated with diammonium phosphate (F_{DAP}), triple superphosphate (F_{TSP}), weed control (W), and fertilization combined with weed control (F_{DAP}W and F_{TSP} W).

	Aboveground biomass				Forest floor	
Effect	Foliage	Bark	Branch	Stem wood	Oi	Oe+Oa
F_{DAP}	**0.043**	0.500	0.081	0.9641	**0.001**	**0.026**
W	0.085	0.265	0.075	0.8423	**0.039**	0.347
F_{DAP} x W	0.244	0.302	0.154	0.3402	0.278	0.829
F_{TSP}	0.159	0.072	0.396	0.658	**<.0001**	**0.010**
W	0.185	0.306	0.311	0.489	0.126	0.091
F_{TSP} x W	**0.006**	**0.028**	0.541	0.095	0.556	0.396

DF =1 for all main and interaction effects

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table A-8. Mean (±SE) P accumulation (kg P ha^{-1}) in aboveground vegetation, forest floor and soil for a 25-year-old loblolly pine stand near Palatka, FL fertilized with diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP}), weed control (W), and fertilization combined with weed control (F_{DAP}W and F_{TSP} W).

	Aboveground components				Forest floor		Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem wood	Oi	Oe+Oa	0-10	10-20	20-50	50-100
C	8.0	1.2	3.4	9.9	7.4	27.4	25.7	13.7	19.1	182.5
	(0.8)	(0.1)	(0.2)	(0.3)	(0.42)	(2.1)	(1.8)	(1.7)	(3.1)	(31.7)
W	8.7	1.4	3.8	12.1	7.2	22.3	31.0	20.8	22.0	212.4
	(1.4)	(0.3)	(0.6)	(2.2)	(0.71)	(2.9)	(1.8)	(3.7)	(5.2)	(52.1)
F_{DAP}	9.5	1.7	3.6	14.5	10	37.8	49.3	21.0	19.9	137.1
	(0.9)	(0.2)	(0.3)	(1.5)	(1.22)	(2.5)	(1.9)	(3.0)	(3.9)	(17.5)

Table A-8. Continued

	Aboveground components				Forest floor		Soil depth interval (cm)			
Treatment	Foliage	Bark	Branch	Stem wood	Oi	Oe+Oa	0-10	10-20	20-50	50-100
F_{DAP} W	11.7	2.1	4.8	17.9	7.1	30.8	34.9	20.2	20.8	138.4
	(0.4)	(0.4)	(0.2)	(3.4)	(0.65)	(3.1)	(2.8)	(2.8)	(2.7)	(20.0)
F_{TSP}	10.5	2.2	3.9	18.3	8.6	36.2	24.6	18.1	25.4	147.5
	(1.4)	(0.4)	(0.6)	(3.3)	(0.85)	(2.5)	(2.0)	(4.2)	(3.1)	(13.7)
F_{TSP} W	12.9	1.9	4.6	15.8	9.1	34.9	33.2	19.3	31.5	120.0
	(1.2)	(0.3)	(0.8)	(2.4)	(1.16)	(3.9)	(3.8)	(3.9)	(4.9)	(18.4)

Table A-9. Statistical summary (ρ values) for main and interaction effects of treatments on P accumulation (kg P. ha^{-1}) in aboveground vegetation, forest floor, and soil for a 25-year-old loblolly pine (*Pinus taeda*) stand in Palatka, FL treated with diammonium phosphate (F_{DAP}), triple superphosphate (F_{TSP}), competition control (W), and fertilization plus with weed control (F_{DAP}W and F_{TSP} W).

	Aboveground biomass				**Forest floor**		**Soil depth interval (cm)**			
Effect	Foliage	Bark	Branch	Stem wood	Oi	Oe+Oa	0-10	10- 20	20-50	50-100
F_{DAP}	0.076	0.077	0.215	0.559	0.101	**0.002**	0.170	0.218	0.948	0.088
W	0.636	**0.043**	0.497	0.399	**0.045**	**0.034**	0.646	0.245	0.599	0.644
F_{DAP} x W	0.426	0.221	0.748	0.405	0.076	0.727	0.320	0.153	0.787	0.672
F_{TSP}	0.060	0.157	0.859	0.153	0.072	**0.002**	0.799	0.595	**0.030**	0.065
W	0.105	0.807	0.399	0.867	0.883	0.278	**0.006**	0.154	0.182	0.971
F_{TSP} x W	**0.037**	0.670	0.771	0.155	0.699	0.516	0.480	0.293	0.572	0.389

DF =1 for all main and interaction effects

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table A-10. End of rotation average for pH and extractable N and P concentrations (mg kg^{-1})) in mineral soils of 25 - year-old loblolly pine stand near Palatka, FL fertilized with diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP}), weed control (W), and fertilization combined with weed control ($F_{DAP}W$ and F_{TSP} W).

Depth (cm)	Soil Characteristic	C	F_{DAP}	W	$F_{DAP}W$	F_{TSP}	F_{TSP} W
0-10	pH	4.6	4.6	4.8	4.5	4.6	4.6
10-20	pH	4.8	4.7	4.9	4.5	4.7	4.7
20-50	pH	5.4	5.2	5.9	5.0	5.4	5.3
50-100	pH	5.1	5.2	5.2	4.8	5.0	4.9
0-10	NH_4^+ (ppm)	50.5	39.2	52.3	48.4	37.3	41.3
10-20	NH_4^+ (ppm)	28.4	16.9	29.0	22.9	30.4	23.3
20-50	NH_4^+ (ppm)	14.5	9.2	7.3	10.4	14.2	19.3
50-100	NH_4^+ (ppm)	23.2	9.2	1.7	8.7	13.6	11.5

Table A-10. Continued

Depth (cm)	Soil Characteristic	C	F_{DAP}	W	$F_{DAP}W$	F_{TSP}	F_{TSP} W
0-10	NO_3^- (ppm)	47.1	44.8	39.8	55.5	38.1	38.5
10-20	NO_3^- (ppm)	49.4	26.8	36.3	36.6	55.6	37.2
20-50	NO_3^- (ppm)	69.6	30.7	19.5	42.9	46.3	46.4
50-100	NO_3^- (ppm)	45.8	34.3	27.5	34.1	52.3	49.7
0-10	PO_4^{3-} (ppm)	1.3	3.4	1.7	2.8	3.6	3.8
10-20	PO_4^{3-} (ppm)	0.4	2.7	1.0	1.4	2.5	1.1
20-50	PO_4^{3-} (ppm)	0.1	0.7	0.4	0.1	0.7	0.6
50-100	PO_4^{3-} (ppm)	4.5	7.6	5.9	9.5	7.6	9.7

Table A-11. Statistical summary (ρ-values) for effects of treatments on soil characteristics (extractable ammonium, nitrate and phosphorus concentration) of fertilization with diammonium phosphate (F_{DAP}) or triple superphosphate (F_{TSP}), weed control (W), and their combination for the soil layers (0-10 cm, 10-20 cm, 20-50 cm, and 50-100 cm) of a 25-year-old loblolly pine stand near Palatka, FL.

Effect	**NH_4^+**	**NO_3^-**	**PO_4^{3-}**
		0-10 cm	
F_{DAP}	0.149	0.478	**0.007**
W	0.293	0.858	0.849
$_{DAP}$ x W	0.471	0.342	0.353
F_{TSP}	0.018	0.451	**0.009**
W	0.543	0.612	0.681
F_{TSP} x W	0.809	0.568	0.902

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table A-11. Continued

Effect	NH_4^+	NO_3^-	PO_4^{3-}
		10-20	
F_{DAP}	0.104	0.120	**0.008**
W	0.532	0.808	0.417
F_{DAP} x W	0.609	0.112	**0.043**
F_{TSP}	0.750	0.587	**0.029**
W	0.591	**0.024**	0.359
F_{TSP} x W	0.524	0.684	**0.033**

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table A-11. Continued

Effect	**NH_4^+**	**NO_3^-**	**PO_4^{3-}**
		20-50 cm	
F_{DAP}	0.637	0.536	0.341
W	0.206	0.141	0.351
F_{DAP} x W	0.082	**0.021**	**0.020**
F_{TSP}	0.112	0.870	0.168
W	0.764	**0.029**	0.841
F_{TSP} x W	0.097	**0.029**	0.461

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

Table A-11. Continued

Effect	NH_4^+	NO_3^-	PO_4^{3-}
		50-100	
F_{DAP}	0.403	0.826	**0.003**
W	**0.016**	0.405	0.112
F_{DAP} x W	**0.019**	0.416	0.798
F_{TSP}	0.985	0.392	**0.010**
W	**0.022**	0.532	0.157
F_{TSP} x W	0.055	0.638	0.764

Effects with bold numbers are significantly different effects (Tukey's HSD at alpha=0.05).

APPENDIX B

STATISTICAL RESULTS (MEAN VALUES): SSPS SITE

Table B-1. Average (±SE) estimates of C (g C kg^{-1}) concentration for untreated carry-over treatments of the soil layers (0-10 cm, 10-20 cm and 20-50 cm) of a 3-year-old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

Treatment	0-10 cm	10-20 cm	20-50 cm
	Bed		
CC	25.6 (7.0)	21.5 (2.7)	12.5 (5.4)
CF	25.1 (8.4)	23.8 (6.1)	6.4 (0.7)
CW	29.5 (0.8)	23.6 (5.7)	10.6 (3.3)
CF W	33.9 (7.1)	28.3 (2.5)	10.4 (1.8)
	Inter bed		
CC	31.4 (1.2)	17.0 (1.7)	3.6 (0.1)
CF	23.1 (4.5)	10.3 (2.1)	2.1 (0.6)
CW	38.1 (4.4)	13.6 (2.4)	2.4 (0.3)
CF W	33.2 (1.2)	16.8 (1.2)	3.3 (0.7)

Table B-2. Average (±SE) estimates of N concentration (g N kg^{-1}) for untreated carry-over treatments of the soil layers (0-10 cm, 10-20 cm and 20-50 cm) of a 3-year-old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

Treatment	**0-10 cm**	**10-20 cm**	**20-50 cm**
	Bed		
CC	0.88 (0.21)	0.73 (0.09)	0.44 (0.15)
CF	0.87 (0.25)	0.77 (0.20)	0.27 (0.03)
CW	1.01 (0.06)	0.9 (0.15)	0.36 (0.09)
CFW	1.10 (0.26)	0.88 (0.10)	0.34 (0.06)
	Inter bed		
CC	1.0 (0.08)	0.56 (0.05)	0.17 (0.02)
CF	0.86 (0.13)	0.39 (0.04)	0.0 7 (0.02)
CW	1.31 (0.23)	0.47 (0.06)	0.06 (0.02)
CFW	1.09 (0.04)	0.53 (0.04)	0.16 (0.02)

Table B-3. Average (±SE) estimates of C: N ratio for untreated carry-over treatments of the soil layers (0-10 cm, 10-20 cm and 20-50 cm) of a 3-year-old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

Treatment	**0-10 cm**	**10-20 cm**	**20-50 cm**
		Bed	
CC	28.6 (1.1)	29.4 (0.6)	26.4 (2.8)
CF	28.1 (1.5)	30.9 (1.1)	24.0 (1.5)
CW	29.4 (1.0)	29.4 (1.5)	28.6 (1.7)
CFW	31.2 (1.5)	32.2 (1.6)	30.0 (1.0)
		Inter bed	
CC	28.7 (1.1)	30.6 (0.8)	22.0 (4.0)
CW	29.6 (1.8)	29.1 (1.3)	28.2 (3.1)
CF	26.4 (1.6)	26.6 (1.0)	21.6 (0.9)
CW	29.6 (1.8)	29.1 (1.3)	28.2 (3.1)
CFW	30.6 (1.0)	31.8 (1.0)	25.6 (2.7)

Table B-4. Average (±SE) estimates of extractable ammonium, nitrate and phosphorus concentrations (mg kg^{-1}) through time for un-treated carry-over treatments of the soil layers (0-10 cm, 10-20 cm and 20-50 cm) of a 3-year-old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

Time	**Depth (cm)**	**Location**	**Extractable N or P**	**CC**	**CW**	**CF**	**CFW**
Start	0-10	B	NH_4^+	52.0 (15.0)	37.9 (15.6)	54.2 (15.4)	57.0 (12.1)
End				213 (22.2)	282 (24.1)	146 (16.4)	207 (71.4)
Start		IB		41.1(14.2)	51.8 (3.6)	45.3 (17.7)	36.4 (6.0)
End				234 (89.6)	211 (41.3)	151 (20.1)	192 (10.7)
Start	10-20	B	NH_4^+	63.7 (16.3)	39.8 (2.4)	44.0 (17.2)	36.3 (9.6)
End				136 (41.7)	214 (42.5)	135 (34.1)	153 (39.1)
Start		IB		59.4 (18.4)	33.3 (3.1)	40.1 (15.2)	50.7 (25.5)
End				97 (17.1)	90 (36.1)	54 (13.8)	80 (13.4)
Start	20-50	B	NH_4^+	77.0 (35.4)	29.4 (10.5)	38.6 (13.0)	25.0 (8.6)
End				34 (1.3)	61 (5.1)	31 (5.8)	47 (0.8)
Start		IB		40.5 (20.0)	23.5 (7.6)	36 (16.9)	15.9 (5.9)
End				27 (4.5)	32 (3.9)	27 (2.2)	33 (6.6)

Table B-4. Continued

Time	**Depth (cm)**	**Location**	**Extractable N or P**	**CC**	**CW**	**CF**	**CFW**
Start	0-10	B	NO_3^-	41.6 (18.6)	14.9 (5.6)	20.0 (4.2)	20.1 (10.0)
End				186 (19.8)	180 (28.0)	200 (23.7)	111 (22.2)
Start		IB		30.0 (20.6)	11.7 (3.8)	11.3 (3.8)	12.9 (2.2)
End				174 (36.6)	161 (50.2)	176 (26.6)	169 (27.8)
Start	10-20	B	NO_3^-	27.2 (6.8)	15.6 (2.1)	14.1 (6.0)	16.7 (4.1)
End				149 (31.2)	162 (10.8)	196 (70.8)	142 (33.0)
Start		IB		31.6 (15.9)	17.1 (3.6)	15.8 (6.9)	14.1 (2.8)
End				137 (12.0)	124 (26.7)	121 (6.8)	106 (18.2)
Start	20-50	B	NO_3^-	17.2 (1.3)	20.4 (11.5)	15.1 (2.6)	16.8 (5.8)
End				74 (26.6)	87 (19.5)	85 (11.7)	114 (12.6)
Start		IB		15.2 (6.2)	12.5 (5.0)	4.1 (2.1)	13.2 (7.2)
End				41 (13.3)	41 (8.7)	21 (8.3)	55 (18.2)

Table B-4. Continued

Time	Depth (cm)	Location	Extractable N or P	CC	CW	CF	CFW
Start	0-10	B	PO_4^{3-}	1.2 (0.1)	1.7 (0.1)	3.1 (1.1)	2.9 (0.2)
End				8.3 (0.2)	8.8 (1.3)	9.1 (1.8)	8.3 (2.4)
Start		IB		1.5 (0.1)	2.5 (0.5)	3.2 (1.6)	1.7 (0.1)
End				10.1 (2.5)	8.5 (2.4)	8.8 (1.4)	8.3 (1.4)
Start	10-20	B	PO_4^{3-}	1.1 (0.1)	1.4 (0.2)	2.1 (0.4)	2.2 (0.5)
End				6.4 (0.5)	6.3 (0.6)	11.4 (4.6)	7.5 (2.6)
Start		IB		1.5 (0.5)	1.0 (0.2)	3.4 (2.7)	2.0 (0.3)
End				4.7 (0.6)	3.4 (1.4)	4.8 (1.6)	4.2 (1.0)
Start	20-50	B	PO_4^{3-}	1.3 (0.6)	1.3 (0.2)	4.5 (2.1)	1.2 (0.4)
End				1.8 (0.5)	2.6 (0.6)	4.0 (1.4)	3.5 (1.3)
Start		IB		2.2 (0.6)	1.5 (0.4)	2.5 (0.6)	1.2 (0.3)
End				0.5 (0.1)	1.0 (0.1)	1.5 (0.9)	1.0 (0.1)

Table B-5. Average (± SE) soil pH across all study for untreated carry-over (CC, CW, CF, and CFW) and actively managed retreated (RF and RFW plots of a 3-year-old loblolly pine (*Pinus taeda*) plantation near Palatka, FL.

Depth (cm)	CC	CW	CF	CFW	RF	RFW
0-10	4.6 (0.1)	4.6 (0.1)	4.7 (0.2)	4.5 (0.1)	4.6 (0.1)	4.6 (0.2)
10-20	4.8 (0.1)	4.7 (0.1)	4.9 (0.2)	4.5 (0.1)	4.7 (0.1)	4.7 (0.2)
20-50	5.5 (0.2)	5.5 (0.2)	5.9 (0.2)	5.1 (0.1)	5.4 (0.1)	5.3 (0.3)

APPENDIX C

STATISTICAL RESULTS (MEAN VALUES): IMPAC SITE

Table C-1. Mean P concentration (g kg^{-1}) in aboveground vegetation, forest floor, roots, and soil for a 26-year-old loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii var.eliottii*) stands near Gainesville, FL treated with fertilization (F), weed control (W), and fertilization combined with weed control (FW).

	Aboveground components				Forest floor			Roots (mm)		Soil depth interval (cm)		
Treatment	Foli-age	Bark	Branch	Stem	Wood	Oi	Oe+Oa	< 2	> 2	0-33	33-66	66-100
Loblolly pine												
C	0.84	0.049	0.007	0.005	0.15	0.39	0.37	0.41	0.40	0.009	0.065	0.085
	(0.03)	(0.003)	(0.001)	(0.02)	(0.01)	(0.02)	(0.02)	(0.04)	(0.06)	(0.00004)	(0.018)	(0.012)
W	0.84	0.046	0.007	0.005	0.15	0.33	0.34	0.53	0.26	0.009	0.079	0.079
	(0.03)	(0.001)	(0.002)	(0.00)	(0.01)	(0.02)	(0.02)	(0.03)	(0.05)	(0.00005)	(0.018)	(0.034)
F	0.89	0.046	0.007	0.005	0.18	0.47	0.38	0.65	0.54	0.010	0.044	0.068
	(0.02)	(0.004)	(0.002)	(0.02)	(0.01)	(0.02)	(0.02)	(0.03)	(0.08)	(0.00004)	(0.004)	(0.009)

Table C-1. Continued

	Aboveground components				Forest floor			Roots (mm)		Soil depth interval (cm)		
Treatment	Foliage	Bark	Branch	Stem	Wood	Oi	Oe+Oa	< 2	> 2	0-33	33-66	66-100
FW	0.91	0.050	0.007	0.006	0.21	0.48	0.43	0.46	0.29	0.010	0.066	0.071
	(0.05)	(0.004)	(0.001)	(0.001)	(0.05)	(0.04)	(0.05)	(0.04)	(0.05)	(0.00005)	(0.016)	(0.016)
Slash pine												
C	0.78	0.045	0.007	0.005	0.13	0.35	0.30	0.36	0.59	0.010	0.053	0.065
	(0.02)	(0.004)	(0.001)	(0.01)	(0.02)	(0.01)	(0.02)	(0.03)	(0.09)	(0.00005)	(0.009)	(0.020)
W	0.76	0.038	0.007	0.005	0.16	0.30	0.24	0.36	0.20	0.011	0.065	0.065
	(0.05)	(0.001)	(0.002)	(0.02)	(0.00)	(0.00)	(0.01)	(0.07)	(0.02)	(0.00005)	(0.004)	(0.015)
F	0.92	0.041	0.007	0.005	0.17	0.47	0.30	0.44	0.72	0.011	0.060	0.067
	(0.06)	(0.002)	(0.002)	(0.02)	(0.02)	(0 07)	(0.02)	(0.04)	(0.16)	0.00004)	(0.006)	(0.023
FW	0.87	0.039	0.007	0.006	0.16	0.45	0.28	0.43	0.24	0.011	0.105	0.078
	(0.01)	(0.003)	(0.001)	(0.03)	(0.02)	(0 04)	(0.02)	(0.06)	(0.05)	(0.00004)	(0.019)	(0.018)

Table C-2. Mean P content (kg ha^{-1}) in aboveground vegetation, forest floor, roots, and soil for 26-year-old loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii var.eliottii*) stands near Gainesville, FL treated with fertilization (F), weed control (W), and fertilization combined with weed control (FW).

	Aboveground components					Forest floor		Roots (mm)		Soil depth interval (cm)		
Treatment	Foliage	Bark	Branch	Stem	Wood	Oi	Oe+Oa	< 2	> 2	0-33	33-66	66-100
Loblolly pine												
C	3.7 (0.7)	0.7	0.1	0.5	0.6	9.7	47.8	2.4	3.2	34.2	337.8	468.4
		(0.3)	(0.2)	(0.2)	(0.1)	(0.3)	(13.7)	(0.7)	(0.9)	(2.2)	(88.0)	(61.1)
W	4.9 (0.6)	1.0	0.1	0.8	1.0	9.6	36.9	0.9	1.6	34.6	408.6	619.5
		(0.1)	(0.5)	(0.3)	(0.2)	(1.9)	(11.4)	(0.1)	(0.5)	2.5)	(100.4)	(92.4)
F	5.6 (0.4)	1.2	0.1	0.9	1.9	15.2	108.3	2.7	4.6	42.3	229.5	370.3
		(0.2)	(0.2)	(0.1)	(0.1)	(2.0)	(22.2)	(0.2)	(0.3)	(1.0)	(11.8)	(55.6)
FW	5.7 (0.3)	1.3	0.1	1.2	1.3	19.7	73.0	0.7	1.7	42.4	325.5	456.8
		(0.2)	(0.1)	(0.2)	(0.3)	(1.4)	(17.8)	(0.1)	(0.4)	(2.3)	(68.2)	(49.4)

Table C-2. Continued

	Aboveground components				Forest floor			Roots (mm)		Soil depth interval (cm)		
Treatment	Foliage	Bark	Branch	Stem	Wood	Oi	Oe+Oa	< 2	> 2	0-33	33-66	66-100
Slash pine												
C	3.3 (0.1)	0.7	0.1	0.5	1.8	9.3	42.9	1.5	3.9	38.8	270.8	425.6
		(0.1)	(0.1)	(0.2)	(0.7)	(1.4)	(3.8)	(0.2)	(0.8)	(2.1)	(40.6)	(66.6)
W	4.5 (0.5)	1.1	0.1	1.0	1.7	9.4	26.1	0.5	1.2	40.8	271.0	434.6
		(0.1)	(0.2)	(0.2)	(0.1)	(0.2)	(3.3)	(0.1)	(0.4)	(2.3)	(19.6)	(50.0)
F	4.7 (0.6)	0.9	0.3	0.7	1.7	12.4	76.7	2.0	4.6	50.3	322.0	450.2
		(0.1)	(0.5)	(0.1)	(0.1)	(1.7)	(3.6)	(0.3)	(1.2)	(1.8)	(27.2)	(35.1)
FW	5.4 (0.3)	1.0	0.1	1.0	2.2	15.1	41.6	0.4	1.5	48.9	557.7	510.0
		(0.2)	(0.2)	(0.3)	(0.5)	(1.5)	(10.8)	(0.1)	(0.7)	(1.5)	(109.9)	(67.1)

Table C-3. Mean (±SE) C, N (g kg^{-1}) and P (mg kg^{-1}) concentrations in soil layers 1-year following a harvest of a 26-year-old loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii var.eliottii*) stand near Gainesville, FL.

Soil depth (cm)	Treatment	C	N	P
	Loblolly pine			
0-20	C	34.1 (5.9)	1.11 (0.19)	0.07 (0.01)
	F	36.6 (2.3)	1.30 (0.03)	0.09 (0.01)
	W	15.5 (2.0)	0.46 (0.06)	0.07 (0.01)
	FW	45.7 (12.4)	1.41 (0.37)	0.12 (0.05)
20-40	C	21.7 (10.3)	0.54 (0.33)	0.07 (0.03)
	F	39.8 (16.2)	1.52 (0.70)	0.15 (0.06)
	W	13.9 (5.8)	0.45 (0.21)	0.06 (0.02)
	FW	25.4 (6.6)	0.82 (0.20)	0.07 (0.02)

Table C-3. Continued

Soil depth (cm)	Treatment	C	N	P
	Slash pine			
0-20	C	26.2 (6.5)	0.70 (0.16)	0.08 (0.01)
	F	30.1 (5.1)	0.80 (0.13)	0.10 (0.01)
	W	29.5 (7.4)	0.73 (0.08)	0.06 (0.01)
	FW	57.9 (24.1)	1.32 (0.41)	0.12 (0.04)
20-40	C	17.9 (4.7)	0.49 (0.11)	0.04 (0.01)
	F	15.1 (5.8)	0.43 (0.14)	0.05 (0.02)
	W	20.8 (6.6)	0.56 (0.15)	0.06 (0.01)
	FW	25.6 (8.2)	0.67 (0.21)	0.10 (0.05)

Table C-4. Mean (±SE) C: N, C: P and N: P ratios in soil layers 1-year following a harvest of a 26-year-old loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii var.eliottii*) stands near Gainesville, FL

Soil depth (cm)	Treatment	C: N	C: P	N: P
	Loblolly pine			
0-20	C	30.7 (1.0)	548.4 (164)	17.7 (4.9)
	F	28.2 (1.1)	418.3 (63.7)	14.7 (1.7)
	W	34.1 (0.6)	218.9 (40.7)	6.5 (1.3)
	FW	32.0 (0.7)	449.5 (186.7)	13.9 (5.6)
20-40	C	28.4 (6.5)	310.7 (8.5)	6.7 (2.4)
	F	29.8 (3.9)	256.7 (20.8)	9.1 (1.8)
	W	31.3 (3.4)	219.9 (48.7)	6.9 (1.3)
	FW	30.6 (0.6)	397.1 (64.9)	13.0 (2.3)

Table C-4. Continued

Soil depth (cm)	Treatment	C: N	C: P	N: P
	Slash pine			
0-20	C	36.9 (0.9)	302.4 (23.2)	8.2 (0.4)
	F	37.6 (0.3)	292.2 (28.6)	7.8 (0.7)
	W	39.1 (5.8)	472.6 (83.4)	12.0 (0.6)
	FW	40.4 (5.9)	440.7 (83.5)	11.0 (2.0)
20-40	C	36.0 (2.4)	386.1 (49.9)	10.7 (1.1)
	F	33.6 (2.2)	343.6 (29.8)	10.4 (1.4)
	W	35.1 (3.6)	349.8 (58.0)	9.9 (1.1)
	FW	37.6 (0.8)	299.7 (47.6)	8.0 (1.3)

Table C-5. Average estimates (±SE) of changes in soil extractable N (NH_4^+ and NO_3^-) (mg N kg^{-1} soil) through time for soil layers 1-year following a harvest of a 26-year-old loblolly pine and slash pine stands near Gainesville, FL

Depth (cm)	Time (days)	Nutrient (mg kg^{-1})	CC	CF	CW	CFW
	Loblolly pine					
0-20	Start	NH_4^+	43.4 (19.3)	50.7 (9.9)	22.8 (10.1)	35.5 (9.4)
		NO_3^-	5.5 (4.8)	6.4 (4.2)	5.1 (2.3)	0.7 (0.1)
	30	NH_4^+	45.2 (12.7)	55.3 (11.7)	41.4 (13.8)	47.8 (1.7)
		NO_3^-	2.7 (0.7)	0.0 (BD)	11.0 (9.60)	0.0 (BD)
	60	NH_4^+	37.1 (4.8)	40.9 (2.0)	36.36 (15.8)	49.2 (3.9)
		NO_3^-	0.0 (BD)	0.0 (BD)	1.8 (1.8)	0.0 (BD)
	90	NH_4^+	42.3 (6.4)	50.1 (13.7)	48.4 (15.7)	67.0 (2.5)
		NO_3^-	0.3 (0.3)	0.0 (BD)	1.3 (0.3)	3.4 (0.4)
	120	NH_4^+	45.9 (8.6)	40.9 (8.7)	47.8 (16.3)	59.8 (4.0)
		NO_3^-	5.5 (2.8)	6.4 (4.2)	5.1 (2.3)	1.7 (0.7)

Table C-5. Continued

Depth (cm)	Time (days)	Nutrient (mg kg^{-1})	CC	CF	CW	CFW
20-40	Start	NH_4^+	54.2 (8.6)	43.6 (13.6)	37.7 (10.4)	35.3 (11.1)
		NO_3^-	19.3 (14.0)	6.8 (3.2)	19.7 (12.4)	6.9 (3.5)
	30	NH_4^+	47.9 (12.7)	44.1 (9.4)	42.7 (8.9)	41.7 (5.1)
		NO_3^-	5.7 (1.7)	1.4 (0.4)	15.9 (13.0)	5.8 (2.4)
	60	NH_4^+	47.7 (14.4)	37.6 (4.8)	30.7 (14.0)	35.8 (9.6)
		NO_3^-	5.0 (0.5)	0.0 (BD)	0.4 (0.4)	0.0 (BD)
	90	NH_4^+	47.1 (17.7)	43.7 (5.6)	36.1 (14.2)	51.7 (8.5)
		NO_3^-	1.1 (0.1)	0.2 (0.2)	1.4 (0.4)	0.3 (0.1)
	120	NH_4^+	46.8 (17.5)	42.4 (8.8)	30.6 (15.4)	42.6 (9.2)
		NO_3^-	19.3 (14.0)	6.8 (3.2)	19.7 (12.4)	6.9 (3.5)

Table C-5. Continued

Depth (cm)	Time (days)	Nutrient (mg kg^{-1})	CC	CF	CW	CFW
	Slash pine					
0-20	Start	NH_4^+	23.5 (10.9)	37.1 (11.0)	9.0 (3.5)	10.5 (1.9)
		NO_3^-	3.2 (2.8)	0.0 (BD)	0.0 (BD)	0.0 (BD)
	30	NH_4^+	35.0 (7.5)	53.8 (7.4)	23.7 (5.0)	40.1 (11.7)
		NO_3^-	0.5 (0.5)	0.0 (BD)	1.5 (1.1)	4.1 (3.4)
	60	NH_4^+	46.0 (6.4)	48.0 (4.7)	27.5 (6.3)	36.0 (11.6)
		NO_3^-	5.0 (5.0)	0.0 (BD)	0.4 (0.4)	0.0 (BD)
	90	NH_4^+	45.1 (9.0)	62.7 (5.2)	44.0 (8.6)	51.9 (15.6)
		NO_3^-	3.4 (0.4)	4.8 (0.8)	3.8 (0.8)	0.0 (BD)
	120	NH_4^+	67.2 (8.7)	32.9 (22.8)	21.5 (1.5)	41.9 (10.0)
		NO_3^-	3.2 (2.8)	0.0 (BD)	0.0 (BD)	0.0 (BD)

Table C-5. Continued

Depth (cm)	Time (days)	Nutrient (mg kg^{-1})	CC	CF	CW	CFW
20-40	Start	NH_4^+	34.8 (13.9)	28.1 (5.8)	18.4 (3.0)	16.3 (2.7)
		NO_3^-	2.3 (1.2)	6.4 (4.5)	4.6 (2.7)	0.6 (0.2)
	30	NH_4^+	41.9 (17.5)	39.6 (10.3)	24.3 (2.7)	44.7 (8.7)
		NO_3^-	8.1 (4.1)	8.0 (5.2)	1.3 (1.3)	3.3 (1.9)
	60	NH_4^+	49.8 (17.1)	33.6 (5.9)	28.1 (1.5)	42.6 (11.8)
		NO_3^-	10.7 (6.9)	10.9 (1.3)	1.8 (1.8)	3.6 (1.8)
	90	NH_4^+	44.1 (7.4)	44.1 (7.4)	35.0 (3.3)	47.5 (2.3)
		NO_3^-	10.7 (5.4)	10.4 (4.4)	0.1 (0.1)	4.1 (2.1)
	120	NH_4^+	33.2 (16.8)	34.9 (5.0)	22.5 (6.1)	38.2 (11.6)
		NO_3^-	2.3 (1.2)	6.4 (4.5)	4.6 (2.7)	0.6 (0.1)

Table C-6. Average estimates (±SE) of changes in soil extractable P (PO_4^{3-}) (mg P kg^{-1} soil) through time for soil layers 1-year following a harvest of a 26-year-old loblolly pine and slash pine stands near Gainesville, FL

Depth (cm)	Time (days)	CC	CF	CW	CFW
	Loblolly pine				
0-20	Start	5.9 (1.4)	6.3 (0.7)	2.3 (0.5)	6.8 (1.3)
	30	5.3 (1.5)	8.3 (0.9)	3.8 (0.4)	6.9 (1.3)
	60	7.8 (1.9)	8.2 (0.5)	5.0 (0.2)	7.9 (1.3)
	90	5.0 (1.8)	6.7 (0.3)	3.6 (0.4)	6.0 (0.8)
	120	6.4 (1.1)	7.3 (0.4)	3.9 (0.6)	7.3 (1.5)
20-40	Start	4.1 (1.4)	6.2 (2.0)	4.0 (1.2)	6.9 (1.4)
	30	5.3 (1.7)	6.6 (2.2)	3.7 (1.7)	5.9 (0.6)
	60	6.6 (2.0)	5.6 (1.5)	4.8 (2.1)	8.7 (1.1)
	90	4.2 (1.3)	6.9 (2.3)	2.9 (1.0)	6.5 (1.3)
	120	4.4 (1.3)	7.0 (2.2)	3.5 (1.1)	6.3 (0.9)

Table C-6. Continued

Depth (cm)	Time (days)	CC	CF	CW	CFW
	Slash pine				
0-20	Start	3.9 (0.9)	5.3 (1.2)	2.3 (0.2)	4.3 (0.3)
	30	5.8 (1.3)	6.2 (0.5)	3.7 (0.6)	5.6 (1.8)
	60	6.0 (1.1)	6.6 (0.7)	4.2 (0.8)	6.1 (1.9)
	90	5.7 (1.5)	5.9 (1.6)	1.9 (0.6)	5.9 (2.0)
	120	5.8 (1.5)	6.1 (0.5)	2.5 (0.2)	5.1 (1.3)
20-40	Start	5.0 (1.0)	5.5 (2.1)	3.0 (0.2)	4.3 (0.3)
	30	5.1 (1.9)	4.6 (0.6)	3.4 (0.3)	5.7 (1.6)
	60	7.6 (2.0)	5.3 (0.5)	4.5 (0.4)	6.5 (1.3)
	90	6.7 (2.0)	5.7 (0.7)	2.4 (0.7)	4.7 (0.7)
	120	6.0 (2.0)	6.6 (1.5)	2.5 (0.9)	4.5 (0.9)